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James Bell Pettigrew's "Design in Nature" and D'Arcy Wentworth Thompson's "On Growth and Form": Two early twentieth-century views of functional morphology

Healy, Matthew David, Ph.D.

Duke University, 1994

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JAMES BELL PETTIGREW'S *DESIGN IN NATURE* AND D'ARCY WENTWORTH THOMPSON'S *ON GROWTH AND FORM*: TWO EARLY TWENTIETH-CENTURY VIEWS OF FUNCTIONAL MORPHOLOGY

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Date: JAN 21, 1994

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Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Zoology in the Graduate School of Duke University

1994

ABSTRACT

(History of Biology)

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Abstract

This dissertation compares two early-twentieth-century works on functional morphology—James Bell Pettigrew's (1834–1908) *Design in Nature* (1908) and D'Arcy Wentworth Thompson's (1860–1948) *On Growth and Form* (1917; 2nd ed. 1942)—and the reception scientists accorded these works at the time and later. Both authors felt that comparative morphologists of the day overemphasized heredity and adaptation as explanations for similarities and differences between species. Both doubted that natural selection could act as a creative evolutionary force. Both were fascinated by geometrical resemblances between different species and even between living and non-living forms; both concentrated particularly on spiral forms in nature. Both works used largely the same set of examples to make the above points.

Despite these books' many similarities, they were accorded vastly different receptions at the time of publication and later. Pettigrew's book was criticized very harshly by reviewers, and soon forgotten. Thompson's book was highly praised by reviewers, and has continued to receive praise from leading scientists throughout the twentieth century; the second edition remains in print today.

The main reason for the difference in receptions accorded these books was the divergent modes of explanation Pettigrew and Thompson invoked for the phenomena they studied. Pettigrew flatly

rejected any form of evolutionary theory, advocating a return to creationist natural theology—updated to incorporate new anatomical and geological data. Thompson's doubts about natural selection were closer to the mainstream, since he did not doubt that evolution had taken place; he merely doubted the ability of natural selection to direct it. Thompson did diverge from most of his contemporaries in preferring to invoke the direct effects of mechanical forces imposed on the organism by its external environment. He considered most contemporary explanations for evolution, including natural selection itself, excessively teleological. Thompson's contemporaries questioned the ability of physical forces to do all that he claimed; modern commentators' reinterpretation regards the forces identified by Thompson as sources of selective pressure, rather than as direct causes of organic form.

Acknowledgements

The members of my Committee—Professor Emeritus John Gregg, Professors Michael McVaugh & Seymour Mauskopf, and James B. Duke Professors Stephen Wainwright & Steven Vogel—have all been very supportive of this project. Steven Vogel has been all an advisor should be; I've tried to emulate his elegant—and award-winning—scientific writing.

The Zoology grad students, particularly the comparative biomechanics group, have been a most stimulating group. Hugh Crenshaw and Carl Heine called *Design in Nature* to my attention (Carl's sister Wendy had pointed it out to him). The Reference Departments at the libraries of Duke, Yale, UNC-Chapel Hill, and the Library of Congress have all been extremely helpful. Duke's ILL Office worked very hard to locate a first edition of *On Growth and Form*, eventually persuading the Medical College of Virginia to loan me a copy. The Zoology Department office staff, especially Anne Lacey, have been most helpful with the logistics of working far from campus. My current employer, Professor David Ward of Yale University, has been most patient in putting up with a part-time computer expert for much longer than either of us expected. Jim & Shirley Goldstein provided housing while I worked at the Library of Congress.

My parents, both of whom have been through dissertations themselves, provided financial and moral support. Last but scarcely least, my wife, Kim Coleman Healy, has provided support and assistance with all aspects of this project. I am not the only person to have noticed how good she is at editing scientific prose; she now does this for a living as Managing Editor of *Oncology Research* and Associate Editor of *Pharmacology and Therapeutics.* Perhaps most important of all, at several points when I thought I would *never* complete this project, she lovingly reminded me of the times when she thought her own dissertation a lost cause.

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Chapter 1

Introduction

For centuries, morphology had been "the very soul" (Darwin, 1859:434) of natural history. Each generation had its own set of questions about the similarities and differences between organic forms; each generation worked from its own set of assumptions. For much of the present century many have seen morphology as rather stodgy and old-fashioned, but there are today signs of renewed scientific interest in morphology. This dissertation is centered around a comparison of two works on morphology that were published in the early part of this century.

Neither James Bell Pettigrew's *Design in Nature* (1908) nor D'Arcy Wentworth Thompson's *On Growth and Form* (1917) was typical of early twentieth century morphology, which was dominated by one theme: the use of similarities and differences between species to determine their genealogical relationships—similarities thought to be hereditary were considered evidence of common ancestry. Many younger biologists found the classification of such similarities and differences sterile and uninteresting, so they turned to other areas of biology. In his book *Life Science in the Twentieth Century* (1975), historian Garland Allen described the reaction of these younger biologists as a "revolt from morphology." Seven years later George Lauder, a prominent modern evolutionary biologist, asserted that morphology in the early 1980s was "undergoing a renaissance" after

"a long period of post-Darwinian dormancy" (Lauder, 1982:xi). Lauder agreed with Allen that "the rise of experimentalism was accompanied by a rejection of many of the explanatory paradigms" (Lauder, 1982:xi) that had been popular in the late nineteenth century, but he asserted that "descriptive morphology did not cease.[1]"

Thompson's *On Growth and Form*—a book that continues to attract scientific interest today—and Pettigrew's *Design in Nature*—a book that has been largely forgotten—are both substantial[2], profusely-illustrated works on morphology that were published early in the "revolt," in the time of "post-Darwinian dormancy." In many respects these two books are strikingly similar. Both works adduce examples from nearly every major taxonomic group of plants and animals, covering a size range from microbes to whales. Both authors were clearly fascinated by certain geometrical shapes (particularly spirals and helices) that could be found in many natural forms—not only in living organisms, but even in many non-biogenic[3] structures. Each book uses literally hundreds of drawings

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[1]Lauder included D'Arcy Thompson in his list of early twentieth-century naturalists who "certainly had a considerable interest in organic form."

[2]Pettigrew's *Design In Nature* comprises three large-format volumes totalling over 1300 pages. The first edition of Thompson's *On Growth and Form*—the edition of greatest historical interest—is over 750 pages long; the second edition of 1942 is several hundred pages longer than the first edition, and the abridged edition of 1961 is about half the size of the first edition.

[3]I use the word *biogenic* to encompass both living organisms (or parts of living organisms) and non-living material that has been laid-down or arranged by living organisms. Many natural structures, such as molluscan shells, foraminiferan tests, and bird or insect nests, are not themselves living though their forms were produced by living organisms.

to show the ubiquity of such shapes in the natural world—and many a drawing from either book could easily have been used as an illustration for the other book. Most important, both authors appear to have had—to a considerable extent—very similar purposes in writing their respective books.

Each author used the geometrical similarities that could often be found in completely unrelated organisms as his main basis for criticizing standard evolutionary theories of the day. In particular, Pettigrew and Thompson questioned the contemporary primacy of heredity and adaptation. They contended that many of the geometrical similarities found in nature could not plausibly be explained as shared inheritance from a common ancestor; nor did they see obvious adaptive significance in such resemblances. Their contemporaries studied organic form primarily as a source of genealogical data. Pettigrew and Thompson—opposing the widespread appeal to historical modes of explanation in morphology—sought universal laws of form.

Striking Differences in Reception

Despite the similarities between these two books, reactions to them from the scientific community in general—in the early twentieth century and in later decades—were sharply divergent.

Contemporary reviews of *Design in Nature* were strongly negative, and the book was soon forgotten. One prominent scientist remarked

of Pettigrew's book that it was "a matter for sincere thankfulness that the time is long past when such a book as this could exert any significant influence on the thought or action of man," (Pearl, 1909) and the other reviews were not much more favorable. Thompson's book, by contrast, was very favorably reviewed in 1917 and is today recognized as a classic in its field. Stephen Jay Gould has described *On Growth and Form* as "a book so broad in appeal that it won [Thompson] an honorary degree at Oxford and, thirty years later, entered the *Whole Earth Catalog* as 'a paradigm classic.'" (Gould, 1983:367). Why, despite the striking similarities between these two books, were the reactions of other scientists so different? This work will explore the reasons for this difference in contemporary reactions to these books.

I believe the main reason why contemporary scientists had such different reactions to these two books—despite their striking similarities—is that Pettigrew and Thompson reached diametrically-opposite conclusions about the *causes* for the morphological resemblances that they both noted. Pettigrew opposed any form of evolutionary theory, advocating a return to creationist natural theology as the only rational explanation for the universal patterns that he saw as pervading all natural forms. Life, for Pettigrew, was a miracle that only God could have created and that only God could sustain (Pettigrew often used the phrase "not only a Creator, but also an Upholder"). Like Pettigrew (and many of their

contemporaries), Thompson expressed reservations about the power of natural selection to produce adaptive evolution. However, Thompson never doubted that evolution had taken place. Unlike Pettigrew, Thompson felt that the proper scientific procedure was to begin by seeking physical explanations for morphological phenomena; only when a biological phenomenon had proven impossible to explain on a physical basis would it be appropriate to invoke other modes of causation. The difference between Pettigrew's teleology and Thompson's physicalism was a major determinant of their divergent contemporary receptions.

Factors Responsible for Difference in Reception

The historical context of early twentieth-century biology made a major contribution to the differences between contemporary reactions to their books. Reviewers saw Pettigrew as rejecting contemporary evolutionism without seriously engaging the arguments that had convinced them that evolution had taken place. They saw Thompson as providing a stimulating critique of standard theories, and found that critique useful and interesting even though they did not accept all of Thompson's conclusions. Since Pettigrew, Thompson, and their contemporaries had been educated in the late nineteenth century, my survey of the historical setting into which these two books fit must obviously begin with a look at morphology in the nineteenth and early twentieth centuries. By and large, I think the reactions of contemporary reviewers to these two books

were quite understandable given (1) then-prevailing views of morphology and (2) the views of morphology propounded by Pettigrew and Thompson. Indeed, despite the many ways in which biology today differs from early twentieth-century biology, the perspective of history largely validates the initial reactions to Pettigrew's *Design in Nature* and Thompson's *On Growth and Form*. Pettigrew's views were not considered useful in his own day, and likely would receive an even less favorable scientific reception if published today. Thompson's views, though not fully accepted in his day, were seen by contemporary scientists as stimulating and valuable even when wrong. Today both the criticisms and the praise for Thompson's book are echoed in even stronger language than in 1917.

If we are to understand how morphologists of the early twentieth century saw *Design in Nature* and *On Growth and Form*, we need to understand the paradoxical state of evolutionism at the turn of the century. In the nineteenth century the old creationist view—that every species had been created by God and immutable thereafter—had been decisively overturned. By 1900 virtually all working biologists accepted evolutionism as a given. However, Darwin's main explanation for evolution—the theory of natural selection—was not very popular among biologists at the turn of the century. A number of alternative evolutionary theories were proposed as resolutions of this difficulty; most of these theories were considerably more teleological than Darwin's theory. Since no single explanation for

adaptation commanded general assent, many morphologists of this period chose to concentrate on those resemblances between species that appeared to be results of common ancestry.

Pettigrew and Thompson were both in reaction against this approach to comparative morphology, with its focus on the historical dimension of organic form. Pettigrew rejected evolutionism in any form, calling for a return to creationist natural theology. Thompson criticized attempts to explain all aspects of growth and evolution in terms of history and teleology, calling for a comprehensive theory of organic form and its growth and evolution in terms of physical forces. Before taking a close look at Pettigrew's *Design in Nature* and Thompson's *On Growth and Form*, in the next chapter I will describe the approach to morphology against which they were in reaction.

> The Catastrophist position in Victorian intellectual history, that 1859 represented a gigantic upheaval in the English philosophical framework, may be losing the struggle for existence.
>
> — Bernard Lightman, 1987

CHAPTER 2

Changing Approaches to Comparative Morphology, 1800–1910

James Bell Pettigrew (1834–1908), D'Arcy Wentworth Thompson (1860–1948), and contemporary reviewers of their books were all products of the nineteenth century. Both authors were born in Scotland—Pettigrew in the small town of Roxhill, Lanarkshire; Thompson in Edinburgh, where his father taught classics. Pettigrew enrolled as a medical student at the University of Edinburgh in 1856, and in 1879 Thompson enrolled as a medical student at that same famous institution—where Charles Darwin had once been a student.

Throughout the nineteenth century there was nearly continuous controversy among biologists over the significance of morphological similarities and differences between species, controversy that accelerated in the latter half of the century. According to Caron (1988), late nineteenth century biologists were quite conscious of participating in a conceptual revolution. The process of change had begun earlier in the century.

The Early Nineteenth Century

Even before 1850 many long-held ideas about the earth and its life had begun to change. "Geologists and cosmologists had begun to challenge the world view of Medieval Christianity," notes historian Peter Bowler, "by postulating that the earth itself and even the universe as a whole had changed significantly over a vast period of time" (Bowler, 1989:4).

Of particular importance in changing the static view of geology was the evidence from stratigraphy, the study of layers in sedimentary rocks. In 1815, William Smith published what many consider to be the first modern geological map of Britain; at around the same time Cuvier and Brogniart were doing similar studies of the Paris basin. Smith "was the first to realize the significance of the fact that different strata had different fossils" (Wilford, 1981:254). As such maps were compiled for other European countries it became clear that the same basic pattern of layers occurred in them all.

By 1850 geologists had pieced together a table of geological strata and associated fossils that was similar in all essentials to that still accepted today. Long before 1800, many fossils had been found that matched no species known to be alive in historical times; a few naturalists, such as Robert Hooke (1635-1702), had argued that some species had become extinct. "However, most naturalists before

the nineteenth century denied extinction" (Porter, 1981:146). By the 1850s the vast majority of biologists and geologists believed evolution had taken place. Cuvier's brilliant reconstructions of extinct fossil vertebrates from his intimate knowledge of their skeletons demonstrated how greatly they had differed from modern species, and the spread of European explorers into the last unknown parts of the Earth made it much more difficult to believe that these species might still exist in some unexplored region of the world.

Comparative anatomy also posed difficult questions. In the early nineteenth century, anatomists were divided between those who stressed the unique characteristics of each species and those who stressed the many similarities between different species, arguing for "unity of type" (Ospovat, 1981:427). Of particular importance was the debate between Etienne Geoffroy Saint-Hilaire (1772-1844) and Georges Cuvier (1769-1832). Geoffroy thought all animals were constructed according to one universal plan; he even attempted to find correspondences between the vertebrate body plan and the arthropod body plan[1]. Cuvier strongly opposed the viewpoint represented by Geoffroy's search for a universal body plan. In the specific case of relating vertebrate morphology to arthropod morphology he convinced most of his contemporaries that, despite a

[1]Arthropods are animals—such as insects and crustaceans—with a jointed exoskeleton. Geoffroy "asserted that every piece of the skeleton of an insect was homologous with some bone" (Russell, 1916:63); many present-day zoologists are unsure whether insect body segments are homologous even with crustacean body segments, to say nothing of vertebrate bones.

few superficial resemblances, arthropods and vertebrates were anatomically incommensurable. In general Cuvier held that the discontinuities between basic body plans of major taxa were too great for comparisons or rankings to be made (Appel, 1987; Bourdier, 1971; Russell, 1916).

Cuvier's most important conceptual contribution to morphology was probably the concept he called "correlation of parts," which viewed an organism as a functional whole. Cuvier supposedly claimed that, at least in principle, a detailed description of an extinct animal could be reconstructed from a single bone (Gould, 1990). This would be possible because functional unity required each and every body part to be perfectly adapted to the organism's way of life. For instance one could conclude from the structure of a single tooth that it must have come from a large predator; if the animal had been a large predator then many other characteristics—such as acute senses and efficient muscles—could also be inferred. If every species were perfectly adapted to its way of life, and if there were one and only one best design for each case, then such conclusions must necessarily follow. Since he regarded each animal as an integrated functional whole, Cuvier denied that any species was related in any way to other species; not only was transmutation impossible because any small modification would disrupt the functional integrity of a species, but the concept known as 'unity of type' was a meaningless abstraction.

In 1848, Richard Owen published a brilliant synthesis drawn from both sides in the debate between followers of Cuvier and followers of Geoffroy. Owen advocated studying each species from two perspectives, which he called "analogy" and "homology." Underlying all the ways in which a group of species, such as the vertebrates, resembled each other, Owen discerned a basic body plan that he termed the "archetype." For Owen this archetype was much more than a simple generalization from many particulars; for him it had an almost mystical significance. In each species, however, the archetype had been modified by functional adaptations. Organisms or parts of organisms that conformed to a common archetype Owen termed "homologous"; organisms or parts of organisms that he saw as adaptations to a common functional need he termed "analogous." Sometimes corresponding parts in two species could be both homologous and analogous; the classic example is provided by bat and bird wings. As vertebrate forelimbs, they are homologous: many parts correspond in detail to each other and to every other vertebrate forelimb. As wings, however, Owen saw them as analogous: the forelimb of the common vertebrate archetype was adapted in two different ways to the requirements of flight.

Owen recognized that adaptation was not perfect; if it were, the homologies would not be evident. Owen was probably not an evolutionist[2]; homology *sensu* Owen was a purely morphological concept. A number of mostly Continental naturalists suggested that

assumptions of common ancestry might provide an explanation for homology.

Probably the first detailed theory of species transmutation was that of Lamarck, published in 1809. Bowler (1989) warns against seeing Lamarck's theory as based primarily on what we today call "Lamarckism": the doctrine of the inheritance of acquired traits. Lamarck's actual theory combined three elements: spontaneous generation, a universal upward trend, and modification by environmental factors. New primitive forms were constantly being formed by spontaneous generation, thereafter slowly ascending the preordained scale of life. Superimposed on the general upward trend were modifications imposed by the environment in which a particular individual lived, modifications that could be inherited by its descendants. Species were lower on the scale had descended from more recent events of spontaneous generation and would in time inevitably rise on the scale. One might say Lamarck's theory replaced the old *scala naturæ* with an escalator of life.

Lamarck's theory seems to have had very little impact in his day. However, by the middle of the century a number of German naturalists had adopted a developmental conception of the species

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[2]It is not clear how Owen's views on transmutation of species evolved during the post-Darwinian era; modern historians disagree with one another on this point. Whether or not Owen came to accept some teleological form of evolution, he certainly did not accept Darwin's theory. His attacks on the *Origin* went far beyond mere scientific disagreement. Freeman (1978:222) characterizes Owen as "the most distinguished vertebrate zoologist" of his day but "a most deceitful and odious man." After 1859 Owen was "probably the only man [Darwin] hated, if he could hate."

based on an analogy with the embryological development of the individual. This is the school of thought that led to Haeckel's famous claim that "ontogeny recapitulates phylogeny," that is, that the life history of an individual repeats the history of its species (Gould, 1977). While these German theories were much more teleological than was Darwinism, they did postulate a branching tree of descent similar in many respects to that accepted today (Lenoir, 1981).

In Britain, mainstream naturalists accepted that every species had been specially created and was immutable thereafter. The first important British account of evolutionary ideas—which appeared in 1844—was published anonymously[3] "to protect its author from the resulting scandal" (Bowler, 1989:111). The book sold very well and went through a dozen editions, but was vigorously attacked by leading scientific and religious authorities. Many have seen the opposition to evolutionary ideas in primarily religious terms, a perception encouraged by such radical evolutionists as T. H. Huxley, a bitter opponent of religious authorities "who made evolution serve his secular interests" (Desmond and Moore, 1991).

However, Bowler (1989) argues that the reasons why most British naturalists rejected European transmutationism were only

---

[3]Many, including Darwin, suspected the Edinburgh publisher Robert Chambers (1802–1883) of being its author. Only after the author's death was public acknowledgement made. When a friend "once asked Chambers why he never owned up to his greatest work. . .he replied, 'I have eleven reasons'" (quoted by Desmond and Moore, 1991:323). Chambers had eleven living children at the time he made this remark.

partly religious. At least as important, in Bowler's view, was an important philosphical difference between Britain and the Continent. According to Bhaskar (1981:199), Hegel and other Continental philosphers viewed history primarily in terms of nations or classes; individuals were important only insofar as they manifested or contributed to the overall "spirit, or Geist," of the age. In natural history, this notion that it was the larger group, not the individual, that mattered led to a focus on the species as an abstract concept, rather than on the individual.

British utilitarian philosophy emphasized the primacy of individual rights and the "social contract." Societies existed to serve the interests of individuals. In social theory this led to Adam Smith's laissez-faire capitalism and the efforts of Whig reformers to remove entrenched privileges that interfered with individual initiative. In biology, British natural theologians saw a benevolent creator as having endowed each individual with exactly those characteristics most useful for functioning in its own environment. Darwin always voted Whig, and his theory of evolution was much more materialist and utilitarian than were the mystical speculations of the German *Naturphilosophen*. While the German evolutionary theorists construed species as abstract "types," Darwin put the unique traits of each individual at the center of his causal model.

1850 to 1910: The Triumph of Transmutationism

Many modern biologists see the development of evolutionary biology in the nineteenth century as a "revolution" comparable to the Copernican Revolution. They see Charles Darwin as *the* leading revolutionary, a man who singlehandedly transformed a central debate (though Wallace, "that perennial afterthought in the Darwinian story" [Desmond and Moore, 1991:669], is usually mentioned in passing). In this view, the main reason why so few early nineteenth century British naturalists accepted the hypothesis then known[4] as "transmutationism" and today known as "evolutionism" was that no credible mechanism for the evolution of biological adaptations had been proposed. As the biologist Richard Dawkins states the problem: "I could not imagine being an atheist at any time before 1859, when Darwin's *Origin of Species* was published" (Dawkins, 1986:5).

As the American geneticist T. H. Morgan described these events fifty years later, in 1909:

> It is sometimes said that the time was ripe for the reception of the ideas formulated by Darwin—it was 'in the air,' as we say—but if so it must have been so attenuated as to be invisible to eyes as sharp as Huxley's (Morgan, 1909:370).

Before 1859, T. H. Huxley (1825–1895) had opposed any form of transmutation theory. Huxley thought his friend Herbert Spencer, "the evolutionist he knew best, needed a dose of expert advice," so

---

[4] *Evolutio* is Latin for "unrolling" or "unfolding." Its older application to embryonic development implied that a pre-existing plan was being fulfilled. According to Desmond and Moore (1991), the first use of "evolution" in something close to its modern sense was in an 1826 paper by Robert Jameson, an Edinburgh professor whose lectures on natural history the young Charles Darwin found "incredibly dull" (Freeman, 1978:175).

they had many arguments on the subject (Desmond and Moore, 1991:323). Once Darwin had explained his theory of natural selection, providing an empirical explanation of evolution, Huxley and many others quickly changed their views. Huxley gave so many public lectures on evolution that he soon became known as "Darwin's Bulldog" (Freeman, 1975; Jensen, 1988) for the fury with which he attacked Darwin's opponents[5].

Unpopularity of Natural Selection in the Early 20th Century

As historians have examined the impact of Darwin's ideas—and no scientific figure other than Newton and Galileo has attracted a comparable degree of historical scrutiny in recent decades—it has become clear that the "revolutionary" account is greatly oversimplified. It is true that few serious naturalists in early Victorian Britain had accepted the idea of "transmutation" or "evolution"; it is true that by the end of the nineteenth century few serious naturalists, in Britain or anywhere else, accepted any form of creationism; and it is very likely true that Charles Darwin had as much responsibility for this major change as did any one person. However, a great many naturalists—including Huxley—in the late nineteenth century did not accept natural selection as the main driving force behind adaptive evolution (Ellegård, 1957; Bowler,

[5]It was a splendid piece of luck for Darwin that the London *Times* chose his friend T. H. Huxley to review the *Origin*, thus assuring the book of at least one favorable notice. The *Edinburgh Review* chose Richard Owen to write an unsigned—and vituperative—review. From internal evidence Darwin and his friends strongly suspected Owen of writing this diatribe, but public acknowledgement came only many years later.

1988, 1989; Desmond and Moore, 1991). Nor was the concept of natural selection universally accepted by naturalists in the early twentieth century.

The historian Peter Bowler calls the early twentieth century, the period when Pettigrew's *Design in Nature* and Thompson's *On Growth and Form* were published, "the eclipse of Darwinism." During this period, "evolution itself remained unquestioned, but an increasing number of biologists preferred mechanisms other than selection to explain *how* it occurred" (Bowler, 1989:246).

Morgan (1909) saw zoologists and botanists of his day as falling into three main groups: the systematists, who simply converted the old search for a "natural classification" into a search for "species-formation and transformation"; the "morphologists, or philosophical anatomists" who studied the historical aspects of form, "applying the theory of evolution to the explanation of group relationships"; and "neo-Darwinians[6]" who

> seem less concerned with the advancement of the theory of evolution than with expounding Darwinism as a dogma ... [For the neo-Darwinians,] to *imagine* a use for an organ is equivalent to explaining its origin by natural selection without further inquiry (Morgan, 1909:371-373).

In Morgan's view, none of these groups seemed very interested in

---

[6]"Neo-Darwinism" in the modern, population-genetic sense did not exist when Morgan wrote this passage. Morgan's "Neo-Darwinians" were a group of his contemporaries who espoused the doctrine of *sola selectione* at a time when other naturalists were seriously questioning the importance of natural selection as a cause of evolution. Darwin himself, with characteristic caution, wrote in the Origin: "I am convinced that Natural Selection has been the main but not exclusive means of modification" (Darwin, 1859:6). In the sixth edition (1872) of the Origin, Darwin complained that many evolutionists had ignored this caveat. Charles Darwin was never dogmatic about Darwinism——or about anything else.

studying how the process of evolution actually took place. Meanwhile, Morgan complained, the physiologists who were studying how organisms worked showed little interest in evolution.

Peter Bowler has noted that "analysis of evolutionary theories in the decades surrounding 1900 is complicated by the fact that so many alternatives were under consideration" (Bowler, 1989:247). At one extreme were the dogmatic Darwinians whom Morgan criticized in the passage quoted above; at the other extreme were those who completely repudiated natural selection, preferring one of many alternative theories. Even Mendelian genetics, which today forms a cornerstone of the modern "synthetic" theory of natural selection, was then seen by many as incompatible with Darwinian evolution.

> The non-Darwinian theories of the later nineteenth century were often progressionist and implicitly teleological: they assumed that evolution was intended to develop toward a particular goal, just as an embryo grows toward maturity. The analogy between evolution and growth allowed many of Darwin's contemporaries to ignore the more radical aspects of his theory—precisely those aspects that modern biologists find most useful. Only after Mendelian genetics had destroyed the plausibility of this analogy did it become possible for a truly materialistic view of evolution to occur. From this perspective, Darwin's theory was a catalyst rather than a true participant in the emergence of nineteenth century evolutionism (Bowler,1986:24).

Morphological Issues and Transmutationism

The great changes discussed above affected nearly every aspect of organismal biology in the nineteenth and early twentieth centuries. As we have seen, morphology played a key role in the development of evolutionary theory, and Darwin recognized its importance: "this is the most interesting department of natural

history, and may be said to be its very soul" (Darwin, 1859:434). Pettigrew's *Design in Nature* and Thompson's *On Growth and Form* were books about morphology, and especially about aspects of morphology that their authors thought had been neglected during the decades following 1859, when Darwin published his *Origin of Species*. Certain issues were of particular importance to Pettigrew, to Thompson, and to the contemporary reviewers of their books.

What is the age of the earth?

By 1850 most geologists accepted the idea that the earth had to be far older than the few thousand years of Scriptural chronology. While actual dates for geological strata could not be determined by any technology then available, the usual working assumption was that such processes as erosion and uplift had proceeded through most of geological time at rates roughly comparable to modern rates. If this assumption was true—and neither geologists nor Darwinian evolutionists were eager to abandon it—then older strata must have ages well in excess of 100 million years. However, in 1868 the physicist Lord Kelvin (in whose honor the SI scale of absolute temperature is named) raised a very serious objection to this "gradualist" geology. The interior of the earth is much hotter than its surface; therefore its crust must be conducting heat away from the interior. Kelvin calculated that no source of energy known to nineteenth century physics could have kept the earth's interior molten for more than about 100 million years—

and this was a generous estimate, allowing for all possible margins of error. Other physicists made similar calculations for the rate at which the sun gives off radiant heat, with a similar conclusion (Bowler, 1989).

This posed a difficult problem for those biologists and geologists who postulated very gradual changes over very long time periods. Darwin remained convinced Kelvin's logic must have some flaw, but could not answer his argument. Not until the twentieth-century development of nuclear physics[7] was an answer to this difficulty found: radioactive elements inside the earth give off the heat required to keep it hot. Among geologists Kelvin's calculation prompted a return to Catastrophism—the theory that past rates of geological change must have been considerably faster than anything observed in historical times. Among biologists it was seen as another serious difficulty for the theory of natural selection: evolution must have been driven by a faster, more direct process than the slow, fumbling, trial-and-error described by Darwin.

What is the significance of homologies?

As we saw above, while the existence of homologous resemblances was generally accepted by the middle of the nineteenth century, their significance was hotly disputed. The old natural

[7]Nuclear physics has also provided methods of using radioactive decay to calculate absolute values for the ages of rocks and fossils—as Pettigrew and others correctly noted, stratigraphy only provided *relative* ages. The earth has turned out to be even older than the nineteenth-century gradualists had thought.

theologians had seen them as proof of design; as a standard text on the subject put it:

> Whenever we see a general plan pursued, yet with such variations in it as are, in each case, required by the particular exigency of the subject to which it is applied, we possess, in such plan and such adaptation, the strongest possible evidence that can be afforded for design (Paley, 1805:230).

The idealists, such as Owen, gave homologies an almost mystical significance that materialists such as Huxley and Darwin found unsatisfying. The general acceptance of transmutationism changed the interpretation of homologies: they were now seen as explainable by the assumption of common ancestry. As Darwin noted in the *Origin*: "on the ordinary view of the independent creation of each being, we can only say that it is so—that it has so pleased the creator to construct each animal or plant" (Darwin, 1859:435).

Darwin felt that "descent with modification" provided a much more satisfying explanation for homologous resemblances between species. Many facts about the taxonomic distribution of homologous resemblances now seemed to make sense under the assumption that most cases of morphological homology (*sensu* Owen) actually represented shared inheritance from a common ancestor, or homology *sensu* Darwin. The mechanism of heredity was still not understood, but morphology clearly had a strong hereditary component. Darwin placed particular stress on nonadaptive, or even maladaptive, traits that he felt could be explained only by shared inheritance from a common ancestor. For example, if lungs had evolved from the swim bladders of fish, this would explain "the strange fact that every particle of

food and drink which we swallow has to pass over the orifice of the trachea, with some risk[8] of falling into the lungs" (Darwin, 1859:191).

Darwin interpreted this odd quirk of anatomy as revealing how "an organ originally constructed for one purpose, namely flotation, may be converted into one for a wholly different purpose, namely respiration" (Darwin, 1859:190). In the decades following 1859, a major focus of anatomical research was sorting out homologies from analogies, in order to construct a classification scheme that described actual ancestry. To evolutionists, classification was not an arbitrary exercise in category-construction, but an attempt to discern the actual historical relationships between species. As Russell noted, "the current morphology, Darwin found, could be taken over lock, stock, and barrel, to the evolutionary camp" (Russell, 1916:247). The search for homologies proceeded as before; only the interpretation of their signficance changed.

What is the origin of functional adaptations?

Among British naturalists, the most popular explanation of functional adaptation before 1859 was intelligent creation. Works on natural theology, such as Paley (1805), argued that in the marvelous adaptations of every living thing to its way of life we see proof of the wisdom and benevolence of the Creator. The natural theologians

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[8]And only after untold eons of evolution would Doctor Harry Heimlich devise his "maneuver" to prevent death by choking.

saw all of creation as an orderly and balanced whole. By the middle of the nineteenth century this worldview was beginning to break down, but none of the alternatives to intelligent creation gained much acceptance among mainstream British naturalists.

As we saw above, even after most British biologists had come to accept evolutionism, the theory of natural selection remained quite unpopular. Many biologists at the turn of the century rejected natural theology but had difficulty putting natural selection in its place as a mechanistic explanation of biological order. The lack of consensus over adaptation, combined with the ease of applying already-familiar methods of classification to the study of homology, led to a nearly exclusive focus on homology in late-nineteenth-century morphological research.

What is the proper place of physico-mathematical methods in morphology?

Throughout the history of the life sciences there has been nearly continual debate over the question of whether living phenomena can be reduced to laws of physics and chemistry. Since there has never been a time when plausible explanations could be advanced for every known aspect of life, answers to this question have always been as much matters of faith as of scientific data.

One particularly important difficulty for those advocating a purely materialistic view of life was the chemical phenomenon of stereoisomerism (Palladino, 1990; Thompson, 1917:416-417; Japp,

1898; Kauffman, 1984:218-220). No purely abiotic method of producing an optically active solution has ever been found. Pasteur, Japp, and many others in the nineteenth century thought this was a fundamental difference between the chemistry of life and all chemical processes not involving life. Vitalists such as Pettigrew would naturally use this as evidence that life cannot be explained in purely physical terms; mechanists such as Thompson had to admit that stereochemistry presented a serious difficulty. Even today, no completely satisfactory resolution of this difficulty has been found (Palladino, 1990).

Most historians agree that physiology was the first area of life science to see the systematic use of experimental hypothesis testing. Modern physiology began in Germany. Nineteenth-century German life-scientists had many heated arguments about whether biological truths could be explained in purely physical terms. According to Lenoir (1981), the conventional interpretation of this debate as "vitalism" versus "mechanism" does not capture its nuances very accurately. Both sides in this German debate conceded that physiology could be understood in purely mechanical terms: the organized matter that comprised an organism did behave in strict accordance with the laws of all matter. However, even if physiology could be understood in purely mechanistic terms, development and evolution could not.

Many nineteenth-century German biologists contended that the

laws of biological development—which applied equally to the development of an individual and to the evolution of a species—could not be reduced to laws of physics and chemistry even if those of physiology could be so reduced. Lenoir contends that this view is not anti-mechanist because many prominent German anti-Darwinians (eg., Von Baer) sought mechanisms of biological development just as did the reductionists led by Helmholtz. The difference was that Helmholtz allowed no appeal to laws outside physical science, while Von Baer insisted that the laws of biological form must differ from the laws of physics in that organisms were goal-directed, or purposeful. Hence Lenoir describes Von Baer and his followers as "telomechanists."

Morphology, unlike physiology, remained largely outside the experimental paradigm. Garland Allen (1975) portrayed twentieth-century biology as a "revolt from morphology" precisely because younger biologists had little patience for a science—morphology—that was still preoccupied with the search for homologies to the exclusion of all else. A number of other historians[9] have disputed Allen's "revolt" model as oversimplified: morphology is by no means dead today, and there was greater methodological continuity than Allen had recognized. Allen himself admitted that he had overstated his case, but still insisted on the basic claim that morphology was

[9]Among Allen's leading critics are Maienschein (1981), Benson (1981), and Rainger (1981, 1989). While Caron (1988) takes a rather different perspective than Allen's, he does see turn-of-the-century organismal biology, on both sides of the Atlantic, as undergoing very rapid conceptual change.

among the last areas of twentieth century life science to see the systematic application of experimental hypothesis testing.

This does not mean that mathematical models and experimental methods were never applied to morphology before the twentieth century. Thompson cited many examples of physical and mathematical analyses being applied to morphological problems in prior centuries. However, these isolated attempts at reducing morphological questions to physical laws never coalesced into a systematic program of research corresponding to the physiological school of Helmholtz and his followers.

These issues—the length of geological time, the meaning of 'homologies,' the origin of functional adaptation, the adequacy of physical explanations—constitute the immediate historical and intellectual context out of which Pettigrew's and Thompson's books emerged and into which they arrived and were judged. The next chapter will examine Pettigrew's views on these matters.

CHAPTER 3

PETTIGREW'S DESIGN IN NATURE

Pettigrew's *Design in Nature*[1] presents, at great length and in staggering anatomical detail, a highly idiosyncratic combination of old and new ideas in geology and comparative morphology. Pettigrew was neither pre-Darwinian nor post-Darwinian but anti-Darwinian. His "progressive creation" model incorporated many aspects of late nineteenth-century geology while flatly rejecting not only Darwinism but the many non-Darwinian evolutionary theories that were so popular among his scientific contemporaries.

His account of life on earth covered a grand sweep of geological time, using data from geology and natural history to show how God had created the many plant and animal species in a long series of separate miracles. Pettigrew accepted as a matter of course many of the conclusions that nineteenth-century geologists and morphologists had drawn from the fossil record. Stratigraphic data had convinced him that life had been present on the earth for millions of years, that many species had become extinct, and that the more advanced species had appeared at later stages in geological history. He accepted the belief of nearly all contemporary

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[1]Full title: *Design in Nature: Illustrated by Spiral and other Arrangements in the Inorganic and Organic Kingdoms as exemplified in Matter, Force, Life, Growth, Rhythms, &c., especially in Crystals, Plants, and Animals. With Examples selected from the Reproductive, Alimentary, Respiratory, Circulatory, Nervous, Muscular, Osseous, Locomotory, and Other Systems of Animals.* London: Longmans, Green, & Company, 1908.

geologists that "the surface of our globe is the product of innumerable forces acting for long periods on heterogeneous substances, and that these forces are at work at the present day" (p. 229).

However, unlike most of his contemporaries, Pettigrew insisted that the truths of natural history required the assumption of an intelligent Designer. "The present work," his Preface begins, "attempts to trace DESIGN, ORDER, and PURPOSE in the inorganic and organic kingdoms, especially the latter" (p. xxiii). For Pettigrew, talk of design was not metaphorical, but literally true: not only had Pettigrew's God created the Universe and set it in motion, but He regularly intervened in its operation. Pettigrew filled his three massive volumes with an exhaustive and often repetitious exposition of this "progressive creationist" viewpoint. Because he was trying to prove that everything known to turn-of-the-century science supported his views, he found it ". . .necessary to deal with Physics, Chemistry, Botany, Zoology, Anatomy, Psychology, and Palaeontology more or less in detail (p. xxi)."

The book's audience

It is not clear what audience Pettigrew had in mind for this book. Throughout the work he addressed the reader in a direct, personal, and rather polemical tone, particularly where evolutionary theories were concerned. "Theories which substitute chance and so-

called natural forces and mechanics for a Creator and Design and for Law and Order," he proclaimed, "are not likely to find favour in the future with thoughtful, educated men" (p. 202). Such a combative tone suggests that the work was not aimed mainly at the scientific community. The preface indicates that the book was aimed at a nonspecialist audience, "written in a popular style" and avoiding technical terminology. The matters discussed, Pettigrew said, had been in recent years of great interest not only to scientists but to "the general public." Each of the four-hundred-and-fifty-seven numbered sections, Pettigrew assured the reader, could be read separately because each section included the background material required to understand the arguments it contained.

The body of the work bears out these statements from the preface. Technical terms are avoided, or defined when they cannot be avoided. Pettigrew used a direct, personal style throughout the book, which is filled with such phrases as "absolutely," "the facts prove," "this wholly forbids," "ignis fatuus," "unjustly relegated," "wholly opposed," and "cannot possibly." This emphatic tone, with its implication that any open-minded reader *must* agree with Pettigrew's views, cannot have encouraged a sympathetic reading from his scientific contemporaries.

As promised, each section is self-contained, resulting in a great deal of background repetition. Pettigrew went to great lengths to make the work understandable for non-specialist readers;

the repeated and lengthy explanations of subjects already familiar to morphologists could not have been intended for specialist readers. However, if Pettigrew meant the book for a popular audience then I have difficulty understanding who was expected to read it. Could he really have intended such a massive three-volume treatise, filled with so much anatomical and physiological detail, for a popular readership? In fact, as we shall see in a later chapter, contemporary reviewers were quite harsh in their criticisms of *Design in Nature*, and I have been unable to find any work published after 1914 that makes more than passing references to it. It may not be clear what audience Pettigrew intended to reach with this book, but it does seem clear that in the end he reached virtually nobody.

Main themes of *Design in Nature*

Five main themes recur again and again in Pettigrew's three volumes. (1) His "**progressive creation**" view of geological history. As mentioned above, Pettigrew accepted—and described in great detail—much of the history of life that naturalists had inferred from the fossil record. In many respects his views were closer to those of mainstream evolutionists than to those of natural theologians before 1859. What Pettigrew rejected was the evolutionary explanation of the accumulated findings: "creation as a progressive work differs from evolution in the sense that the different types of plants and animals which prevailed in the past

[were] produced separately [by divine fiat]" (p. xxx).

(2) Pettigrew considered **common design**, rather than common function or common ancestry, to be the best explanation for many of the similarities between different species. He rejected the basic distinction most comparative anatomists made between analogy and homology, and he rejected the evolutionary conclusions that they drew from homologous resemblances. He adduced a truly staggering amount of anatomical data to support his contention that many morphological similarities could not be explained by any evolutionary theory, but only by the assumption of Divine Design.

(3) Pettigrew represented Divine Design as the only reasonable basic for an explanation of biological **adaptation.** He contended that "it is more reasonable to believe in a First Cause and Design than it is to leave everything to a fortuitous concatenation of circumstances" (p. xxvi). "It has been customary of late years," he complained, "to ignore a First Cause and the Design which a First Cause implies" (p. xxvi).

(4) Pettigrew felt that evolutionists grossly overstated **the effects of environmental influences** on living organisms:

> The time has come when the subject of environment, irritability, and external stimulation must be reconsidered. . .environment does not act as a cause in the strict and proper acceptance of that term, and does not, however great the time allowed, alter plants and animals beyond recognition (p. xxv).

Over and over, in various ways, Pettigrew portrayed organic form and biological activity as resulting from forces internal to the

organism. "Living things," he contended, "are always superior to their surroundings" (p. xxv).

(5) Pettigrew opposed **mechanistic and reductionistic approaches** to the study of living organisms. He felt that experiments on isolated parts violated the integrity of the organism, and that life transcended physical laws. Because God had "superadded the mysterious principle of life" (p. 1069) to dead matter, biologists should not use methods taken from the physical sciences:

> The mechanical treatment of living plants and animals as if they were automatic machines has great attractions for a number of enthusiastic modern physiologists. They pride themselves on obtaining what they are pleased to designate *exact results.* They are ambitious to measure, to weigh, to demonstrate (p. 241).

Because there is so little overall organization in Pettigrew's three volumes—for instance the hundreds of numbered sections are not grouped into chapters—I judge the importance to him of a topic by the frequency with which he returned to it[2]. The above five themes encompass nearly all the recurring topics in Pettigrew's three volumes.

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[2]One topic of obvious importance to Pettigrew is largely omitted from this dissertation: bird flight. Pettigrew's many descriptions of bird flight do not seem very relevant to the present study for three reasons. (1) His studies of flight were purely descriptive; as such they have little bearing on the conceptual issues of greatest importance to this study. (2) Thompson's analysis of flight is very brief and is not central to his main themes. (3) During the nine years between Pettigrew's death and the publication of Thompson's book, aircraft progressed from experimental prototypes to weapons of war; therefore these authors were writing about flight in very different historical and technological contexts. Kelly (1950) quotes Wilbur Wright as comparing bird flight to a magician's trick: only after you've figured out how to duplicate the trick do you know what to look for when you watch it being done.

Progressive Creation Best Explains the Fossil Record

Pettigrew's combination of geology and the Bible is not typical of his or any day. He did not interpret the Scriptures literally, as had most natural theologians in the early nineteenth century; nor did he dismiss the Bible as having little direct relevance to scientific questions. Most turn-of-the century scientists (and many turn-of-the-century theologians) regarded science and religion as independent fields of inquiry: scientific questions were to be answered only with scientific data, and religious questions were beyond the ken of science. Pettigrew was an exception. He insisted that the Bible still could be regarded as a serious scientific work when properly interpreted—in a manner consistent with the hypothesis of successive stages of creation over millions of years but not consistent with any form of evolutionism.

"The view [of geological history] here advanced," he wrote,

> accords, on the whole, with the account given in the Old Testament. . .the seven, or rather the six days. . .evidently represent six epochs of time; each period being undetermined, and as far as Man is concerned, indeterminable. That the six days of Scripture do not mean six ordinary days of twenty-four hours each goes without saying (p. 235).

Pettigrew recognized that while biology and geology had changed radically in the nineteenth century, so had Biblical scholarship:

> the advent of the higher biblical criticism[3], and the rapid strides made of late years by science. . .make it imperative to treat the Old and New Testaments as historical in character as well as religious and moral, and to modify dates, and, in some instances, even to question outstanding events (p. 1328).

While Pettigrew was willing to exhibit some degree of

flexibility in Biblical interpretation, he was not ready to disregard Scripture completely in his account of earth's history. The key points made by the Bible remained, in his view, as valid as ever. God had planned and set in motion the processes that led to the creation of the world, and He had created each and every species, living or extinct, in a separate miracle. All of history had been predestined[4] according to a divine plan, and the highest civilizations throughout history had been monotheistic. Western European civilization, the most advanced of all, was Christian—and evolution was a pernicious doctrine that could undermine that faith, destroying the moral certainties which supported Western civilization.

For the most part, Pettigrew relied primarily on scientific data to prove the main points of *Design in Nature*; his citations of Scripture were adduced to demonstrate how reason and revelation were

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[3]"Higher criticism" is a now obsolete term for an approach to Bible scholarship that began in nineteenth-century Germany: the use of historical research, linguistic analysis, and literary criticism in an attempt to understand the Biblical texts as they had been understood *in the context from which they came.* Such studies have convinced most Bible scholars that the Biblical texts were *not* intended to be read literally, but have not produced much consensus on how they *should* be read. (MacGregor, 1989: entries on "Higher Criticism," "Hermeneutics," "Formgeschichte," "Criticism," & "Textual analysis.")

[4]*Design in Nature* is not primarily a theological work, and I have not been able to find any conclusive information concerning Pettigrew's denominational affiliation. His frequent allusions to predestination were certainly not inconsistent with the Scottish Calvinism of Knox and his descendants. As Pettigrew wrote,

> The doctrine of predestination as here recorded directly raises the question of 'necessity' and of 'free will,' but into this I need not enter further than to say that man cannot be granted a free will and a free hand in any other sense that it is granted to all created things. . .all things in the ultimate sense are fore-ordained and foreseen. . .anything short of this would mean an end of law and order, and a reign of anarchy and confusion (p. 235).

in agreement. However, on "the origin and career of Man" (p. 1324), Pettigrew seems to have come close to conceding that his views might go beyond what purely scientific data could establish:

> if the authority and teaching of the Old Testament and the possession by Man of an extraordinary nervous system and brain be set aside, the preponderance of evidence, many are inclined to believe, is in favour of a lowly origin[5] (p. 1324).

Beyond his disdain for evolutionism in general, Pettigrew was especially critical of claims for human evolution. Old skeletons proved that human morphology had not changed significantly for thousands of years, and the differences between man and apes were too great for evolutionists to explain. Such "missing links" as the recently-discovered Neanderthal skull Pettigrew dismissed as degenerate individuals of *Homo sapiens*.

According to Pettigrew, there were two theories regarding the origin of humanity: gradual ascent from a "lowly origin," which many of his contemporaries accepted, versus the story told by the Bible—creation as a perfect being, then the Fall from Eden, leading to a descent into savagery followed by a slow return to civilization. Pettigrew held that the latter view was to be preferred on the authority of Scripture, since the former view could not be proven. He rejected "the practice of certain scientists and laymen (the so-called agnostic school) of late years to ignore" the evidence of Scripture, which "certainly cannot be pooh-poohed" by "agnostic science" (p. 1331). Even if we do accept that much of the

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[5]"Man still bears in his bodily frame the indelible stamp of his lowly origin" (Darwin, 1871:405).

Bible is parable or allegory, he contended, "the sacred writings lose none of their precious value by not being interpreted literally in every case" (p. 1329).

Pettigrew's main purpose in relating Biblical views to scientific and historical data seems to have been to acknowledge the validity of geological and paleontological evidences for a much longer history than a literal reading of the Bible would permit, without accepting the divorce of science and religion.

Over a very long period of time[6], Pettigrew conceded, as the earth's physical conditions had changed, so had its biota. More and more advanced species of plants and animals appeared; many, but not all, of the primitive species became extinct. Pettigrew's geological narrative would not have been controversial in his own day; it was a fairly standard account of earth's past as revealed by the fossil record. Not only did Pettigrew accept the standard story, but in geology at least he also accepted the standard mode of explanation: the slow operation of such physical phenomena as erosion and vulcanism over millions of years. Pettigrew did insist that the physical mechanisms of geology had been created and set in

[6]Pettigrew seems to have been thinking in millions of years, not tens of millions of years; certainly not the "hundred or more millions of years" advocated by some evolutionists, which "flout human experience, history, and even the geologic record" (p. 204). Concerning the time element of geology, then, Pettigrew was perhaps somewhat conservative but not entirely outside the mainstream of his day. Oddly enough, Pettigrew never mentioned Kelvin's calculation (described in the previous chapter), which many geologists of his day considered the strongest evidence that the earth was less than a hundred million years old.

motion by divine fiat, for the purpose of creating a world hospitable for life.

It was in regard to the biological side of this story that Pettigrew parted company with most of his scientific contemporaries. Each living species, Pettigrew insisted, had been created by God in a separate miracle, though they had been created at many different times over a very long period, not in the Biblical seven days. Pettigrew drew on the fossil data to support several specific arguments against evolution.

First, Pettigrew used fossil data to show that "progress and advance" were by no means universal. He understood evolution as postulating a law of universal advance for every species. However, some species had not advanced: "Huxley, with characteristic candour, admits the extreme persistence in certain cases of various types of plants and animals" (p. 204). Pettigrew considered such persistence of types strong evidence against evolution:

> the existence of the simplest and most complex plants and animals in the same place and time goes against the belief that the more complex plants and animals are manufactured directly or indirectly from the more simple or rudimentary ones. It also goes against the idea that plants and animals are capable of indefinite improvement. If this were so, and creation was non-progressive and confined to one period, such is the extreme age of the earth, [that] the stock of rudimentary plants and animals would long ago have been exhausted—only the most perfect plants and animals remaining (p.232).

The reader will recall from the previous chapter that for just this reason Lamarck had postulated the continual appearance of new lower forms by spontaneous generation. By Pettigrew's day most

naturalists agreed that if spontaneous generation had ever taken place it had probably been so far back in the distant past as to leave no trace in the fossil record; they generally followed Darwin's example and avoided speculating on the ultimate origin of life on earth, leaving the question of past spontaneous generation open. Pettigrew flatly rejected the possibility of spontaneous generation at any time past or present.

Second, Pettigrew contended that each and every species was perfectly adapted to its time and place; modern species are different from extinct species because they were made for different stages of God's plan:

> the plants and animals, moreover, had to be specially constructed to meet the exigencies of the earth and its climate at different periods. . .while geology points to the production of the lower plant and animal forms before the higher, this fact (if fact it be) does not indicate imperfection or want of power in the Creator. (p. 231).

Third, Pettigrew advanced the argument, still popular with fundamentalist critics of evolution today, that the gaps in the fossil record[7] were too great for evolutionists to explain away. "Like other evolutionists," Pettigrew complained,

> Huxley avails himself of whatever connecting links exist or may come to hand, and at the same time endeavors to show that the geological record, from the nature of things, can never be perfect. He indeed emphasizes this point. This is at once an ingenious and a clever device. If an advocate of evolution be permitted to employ such [links] as exist. . .and to say, when the connecting links fail him, that the geologic record is imperfect, he gains a double advantage: he gets credit for what is, and he claims credit for what, there is every reason to believe, is not (p. 204).

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[7] "The extreme rarity of transitional forms in the fossil record persists as the trade secret of paleontology" (Gould, 1980:181).

Comparative Anatomy Proves Common Design

Pettigrew rejected the distinction between homology and analogy and the whole line of argument for evolutionary relationships derived from it. He complained that "slight differences" between species were "unduly magnified when they are intended to support evolution, much greater differences being glossed over or altogether omitted when they do not favour that doctrine" (p. 203). He placed particular stress on the fact that "organic structures which apparently have nothing in common do nevertheless greatly resemble each other" (p. 90). Some of these resemblances, such as similarities between "locomotor structures," were clearly functional.

However, many patterns of form that particularly interested Pettigrew had neither obvious adaptive significance nor any evident connection with taxonomic relationships. Through numerous examples, Pettigrew showed some remarkable similarities not only between organic species but even between them and nonliving structures. For instance, Pettigrew showed side by side drawings of electric sparks, blood vessels, and various plants: these branching patterns, he contended, demonstrated the presence of a common law of "dendritic arrangement" in nature, which he attributed to a common Creator. Pettigrew made similar claims for "linear" and "segmented arrangements," "radial" and "concentric arrangements," "hexagonal arrangements," and above all, "spiral arrangements." Pettigrew's

views on "spirality" will be explored in detail in chapter five.

The drawings, mostly by a professional illustrator working under Pettigrew's supervision, are uniformly excellent, and the vast range of examples certainly do establish that certain shapes—such as spirals—are widespread in the living world.

> If proof were wanting of the intimate relations subsisting between the inorganic and organic kingdoms, and of the unity of plan which pervades all nature, these remarkable coincidences in spiral formations are well calculated to supply it (p. 14).

The reason for such unity, Pettigrew insisted, was that everything in Nature came from a common Designer.

Pettigrew asserted that the spiral and other resemblances running through the living world proved that all of creation was subject to common underlying laws. However, he made no attempt to identify any such "laws." *Design in Nature* contains no mathematical descriptions of these common forms, even in cases where detailed mathematical descriptions had long been known. Nor did Pettigrew ever provide any hypotheses that could be tested experimentally, though he sometimes attacked the hypotheses proposed by others. Indeed it is hard to see how Pettigrew's views could be tested experimentally, given the references to miracles and non-physical forces in his system. For Pettigrew, similarity of shape was, in and of itself, positive evidence for the existence of universal laws of shape.

Biological Adaptation Proves Divine Design

As Pettigrew well knew, the notion of an intelligent Designer was no longer taken very seriously by his scientific contemporaries. Pettigrew was not alone in his discomfort with natural selection, but he was nearly alone in advocating a return to the design hypothesis.

By 1900, most biologists had accepted that shared imperfections were the best evidence for shared ancestry; shared adaptations could be explained by various evolutionary theories or by reference to divine creation. When two species shared a trait that appeared to be adaptive, that could be explained in a variety of ways. As we saw in the last chapter, while there was general agreement among early twentieth-century naturalists *that* evolution had taken place, there was heated dispute over *how* adaptations came to be. When two species shared a number of nonadaptive or even maladaptive peculiarities, there was general agreement that this was evidence for shared inheritance from a common ancestor.

Pettigrew, by contrast, placed great stress on the perfection of biological adaptation. He put heavy emphasis on the sense of wonder that anatomy aroused in him. For him, nature was filled with adaptations perfectly meeting the needs of organisms.

Pettigrew was particularly critical of the claim that bats were more closely related to mammals than they were to birds. He

felt that the similarities between bats and birds were much greater than the similarities between either group and terrestrial vertebrates. He felt that evolutionists were deliberately choosing to base their classification schemes only on selected traits that supported their theories:

> As a matter of fact, the changes and modifications introduced into the animal series because of modifications in their organs of locomotion are much greater than the data usually relied upon for proving the doctrine[8] of evolution and descent (p. 219).

Pettigrew contended that biological adaptations were too perfect for such a random, uncontrolled process as natural selection to explain. Darwin, according to Pettigrew,

> assumes that perfection in plants and animals can only be attained by altering, modifying, and remodelling—a somewhat impotent conclusion considering the extraordinary perfection of nature as a whole. Admitting, however, that the altering, modifying, and remodelling actually occur, they can only take place in one of two ways: either through the agency of a Creator. . .or the plant and animal must possess in themselves, as apart from a Creator, the power to alter and modify themselves *ad libitum*; a power the possession of which. . .I am prepared to dispute (p. 689).

While Pettigrew attacked evolution in many ways, no single idea drew more of his scorn than that of natural selection. "If 'Natural Selection' means anything," he trumpeted,

> it means, as I have already stated, God Selection. The abstract term 'Nature' means Nature's God, and Natural Selection while it ignores cannot get rid of the First Cause. . .plants and animals have no power of themselves or in themselves to select and perpetuate their good properties and qualities to the exclusion of their bad properties and qualities. Neither can a mechanical unintelligent environment do this. . .it follows that selection, if it ever occurs, is made by an intelligent First Cause. There is no getting away from this conclusion (p. 693).

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[8]Pettigrew often used the word "doctrine" when speaking of views he disputed. He rarely used the word with reference to his own views.

Evolutionists Exaggerated Environmental Effects

In Pettigrew's view, both reductionistic physiology and Darwinian natural selection depicted organisms as passive, inert things at the mercy of their environments. The latter, he declaimed over and over, was ridiculous. Every aspect of organic structure and function proved that life was controlled and directed by guiding forces internal to itself.

When a seed grows into a plant, or an embryo into an adult, Pettigrew emphasized, the signficant result is a complex organism nearly identical with its parents and far more complex than the tiny quantity of matter from which it began. Furthermore, the seeds or zygotes of vastly different species are often nearly identical at the start: "Mere force, however gentle or violent, cannot convert practically identical matter into something other than itself" (p. 349). Pettigrew described the development of many species in great detail to support his contention that the whole process was goal-directed.

These developmental processes were directed in such a manner that types bred true. No amount of selective breeding by humans had ever produced a new species, and "like begets like in endless sequence" (a phrase Pettigrew used in many places). Pettigrew emphasized that the variation within a species always stayed within very definite limits; we do not see a continuous distribution of

forms but distinct types wherever we look.

At every stage of growth, the physiology and behavior of each individual acted to maintain its form and function despite great environmental changes. Living organisms, in Pettigrew's view, were always the masters of their environment. They actively took what they needed from the environment and expelled what they did not need.

Animal behavior was always directed towards a goal; even plants could move (though more slowly) towards predetermined goals. "It is difficult to deny to the sensitive plant a low form of cognition, and the power of voluntary movements" (p. 786). Pettigrew devoted nearly half of Volume II to long, anecdotal accounts of "intelligent" behavior in many different animal species. Unlike many modern creationists who stress the differences between human and animal intelligence, Pettigrew stressed the similarities. For him, intelligence was a matter of degree and not of kind; he ascribed emotions and intentions to even the simplest organisms. Pettigrew denied that any "voluntary movement" in the living world could be explained in terms of instinct and automatic response to "extraneous stimulation."

A typical example of Pettigrew's views on animal intelligence is how he explained the orderly actions by which bees made a honeycomb. For Pettigrew, the ultimate source of all goal-directed

behaviors was the Divine Intelligence:

> As the bee cannot be credited with an acquaintance with Euclid, the only explanation that can be given is that the First Cause works in and through the bee, or has conferred on it the necessary intellectual and reasoning powers. . .Everything is designed. . .they work according to a given plan as certainly as if they were embodying. . .all the paraphernalia of modern architecture (pp. 923–924).

Pettigrew praised the mathematical perfection of honeycombs, but his lengthy and detailed description of them contained none of the mathematical analyses of their geometry that had been published during the nineteenth and earlier centuries.

Darwin had not claimed that natural selection was the only cause of adaptive evolution, but only that it was "the main but not exclusive means of modification" (1859:6). He had devoted many pages of the *Origin* to attempts at explaining how various instincts—hive-building in particular—could have evolved by natural selection. Many of Pettigrew's contemporaries doubted the importance of natural selection, but most still conceded that biological adaptations—including instincts—were at least partly caused by environmental factors. Pettigrew did not.

Pettigrew's Opposition to Mechanistic Models

Pettigrew's vitalism led him to oppose all mechanical explanations of biological phenomena. *Design in Nature* contains numerous attacks on mechanistic models. Pettigrew began each attack by describing the anatomy of some structure in great detail. After this he would recount a then-popular physical model of its

operation, emphasizing aspects that this model could not—in his view—explain. From the failure of *this* mechanical model to account for all aspects of structure and function, he would go on to assert that *no* strictly mechanical theory could possibly account for that phenomenon; it must therefore be at least partly produced by vital forces outside those known to the physical sciences.

Pettigrew did not deny that physical laws usually *applied* to life, but he rejected the notion that such laws *explained* it. "The vital forces," he contended, "control the physical forces within certain limits to a desired end" (p. 433). The fact that "the organic kingdom avails itself of inorganic power" (p. 455) did not mean that organic phenomena were limited to physical power:

> The forces generated by nerves and muscle are vital in nature. . .it is not doubted that the work performed by living muscle resembles in its results, that performed by physical force, say that exerted by a steam engine. The mode of production of the two forces is, however, entirely different. Similarly, the force produced by living brain substance cannot be identified with any known physical force. No physical force can control, direct, and guide other forces. The directive force inhering in brain is a thing *per se*; the product of life (p. 766)

However, though Pettigrew asserted that some aspects of brain function were impossible to explain by reference to physical forces alone, he was not (to use his own term), an "immaterialist":

> While the great majority of anatomists and physiologists have no difficulty in associating all manifestations of intellect with the brain and certain molecular changes occurring in the nerve cells. . .it is otherwise with those who reject matter as a substratum of intellect. . .who maintain that the mind is immaterial in its nature. It is interesting to compare the views of so-called materialists and immaterialists. . .That mind is the product of an immaterial something located in the brain is mere hypothesis—a doctrine which derives no support either from observation or experiment. . .some have thought that if the mind is material there can be no immortality of the soul. This, however, does not follow, as matter, like force, is indestructible (p. 784).

Pettigrew presented fourteen "proofs that the brain is the organ, apparatus, or laboratory of the mind" (p. 767)—that is, the mind, while depending for its operation on "vital forces," was *manifested* in physical substance. This mixture of the material and the vital is quite characteristic of Pettigrew's thought.

Another example of the way in which Pettigrew combined mechanical and vitalist views is his discussion of the bicuspid and tricuspid valves in vertebrate hearts. These valves, as Pettigrew explained, are the most important valves in the entire vascular system: they allow blood to flow from atria to ventricles between contractions of the ventricles, but prevent blood from flowing backwards during ventricular contraction. In Pettigrew's day various disorders of the heart valves were often fatal; even today their replacement by artificial valves is by no means free of danger to the patient[9].

Preceding Pettigrew's discussion of heart valve physiology are more than thirty pages on the detailed anatomy of these and other

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[9]A relative of mine lived for many years with a plastic heart valve; without it he would probably have died much sooner, but a healthy natural valve would likely have kept him alive still longer—artificial valves are not nearly as good as the original equipment. Depending on one's biases, the performance of artificial heart valves could be interpreted as evidence for or against Pettigrew's vitalism. If one agrees with most physiologists that heart valves are mechanical in operation, then one could argue that artificial heart valves demonstrate that strictly mechanical valves can work. If one favors Pettigrew's vitalist view, one could argue that no artificial heart valve is a perfect replacement for a natural valve. Of course a mechanist could retort that artificial heart valves are steadily improving and might some day equal—or even surpass—the performance of the real thing. In the absence of such perfect artificial valves, predictions of whether such can be built are matters of faith as much as of scientific data.

valves in the vertebrate circulation. Since Pettigrew was a first-rate anatomist, his descriptions are of a very high quality indeed. As with all of Pettigrew's anatomical descriptions, these descriptions are punctuated with rapturous hymns of praise for their exquisite beauty and complexity. Pettigrew contrasted two theories about their function. In his day, most physiologists accepted a purely mechanical explanation of how these valves opened and closed: they acted like the check valves in any pump, being passively operated by fluid pressure. An older theory was that the papillary muscles and chordae tendineae, which run from the atrial wall to the valve flaps, opened and closed the valves.

The role of the papillary muscles and chordae tendineae was, according to most authorities of the day[10], only to prevent the valves from opening out the wrong way: "the chordae tendineæ acting mechanically, like so many stays, to prevent eversion of the segments in the direction of the ventricles" (p. 561). Pettigrew did not deny that fluid forces had some effect on the operation of heart valves, but he emphatically denied that mechanical forces alone could account for their operation. For one thing, they were much more complex than the semilunar valves in the veins; surely God would not have designed them that way if their function was as simple as that of venous valves. More important, the heart valves

[10]This view—that papillary muscles do not themselves play any role in the opening and closing of heart valves—is still accepted in modern textbooks (including Vogel, 1992; Vander, Sherman, and Luciano 1990; and several editions of *Gray's Anatomy*).

were truly vital to life itself. No purely mechanical valve could work well enough to perform such a vital purpose. This is nineteenth-century natural theology turned on its head. As we saw in the previous chapter, Paley and his successors had argued that the apparent perfection of life provided strong evidence for purpose and design in the universe. Pettigrew here argued that complexity of structure implied purpose, given his fundamental assumption that all aspects of living structure manifested God's purposes.

In the example of heart valves, as in so many other cases, we see Pettigrew making expert use of the latest available anatomical and physiological data while rejecting the conclusions his contemporaries had drawn from such data. In the next chapter we will see how D'Arcy Thompson would use largely the same data as had Pettigrew to criticize contemporary evolutionary orthodoxy. Like Pettigrew, Thompson had views on morphology that were a highly idiosyncratic combination of old and new ideas. However, Thompson diverged from his contemporaries in a very different direction.

CHAPTER 4

Thompson's On Growth & Form

In some ways Thompson's views on morphology, as expressed in his book *On Growth and Form*[1], were considerably closer to the mainstream of early twentieth-century morphology than Pettigrew's views had been. While Pettigrew had firmly opposed evolution, Thompson—like most of his contemporaries—scarcely doubted that evolution had taken place. In an age when mathematics and physical science were becoming increasingly important in biological research, Pettigrew had made virtually no use of mathematics in his study of natural forms. Thompson, by contrast, devoted most of his book to mathematical analyses of biological forms. Pettigrew had been sharply critical of reductionistic experimental physiology; Thompson saw such physiology as an example that morphologists should strive to emulate.

Thompson did have his doubts about natural selection[2], but as we saw in Chapter 2 such doubts were far from rare at the turn of the century. In other ways Thompson's views were by no means typical early twentieth-century biology. Thompson, like Pettigrew,

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[1]Unless otherwise indicated, all references in this chapter use the pagination of the first edition, published by Cambridge University Press in 1917.

[2]By 1942—when the second edition of Thompson's *On Growth and Form* was published—the scientific consensus had changed. Thompson never accepted the "modern synthesis" of Mendelian genetics, natural selection, and population biology; he remained skeptical of both natural selection and Mendelian genetics.

thought that contemporary morphologists placed far too much weight on the concept of homology (though, unlike Pettigrew, Thompson did concede that some alleged cases of homology, *sensu* Darwin, had a sound basis in the principle of heredity). As had Pettigrew, Thompson gave particular attention to geometric shapes, such as spirals, which were distributed among species in ways that did not seem to fit then-popular evolutionary theories. Despite his praise for experimental physiology[3], Thompson—like Pettigrew—was not himself an experimentalist in the modern, hypothesis-testing, mode. His approach to the study of organic form was dominated by the description of dead specimens in a very nineteenth-century mode. Above all, Thompson felt that most contemporary theories of evolution—Darwinian and non-Darwinian alike—retained far too much of the teleology that had characterized nineteenth-century natural theology.

On the subject of teleology Thompson was farther from Pettigrew's creationist views than were most of his contemporaries.

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[3]"Between the physiology of Haller, fine as it was," Thompson remarked, "and that of Helmholtz, Ludwig, Claude Bernard, there was all the difference in the world" (p. 2). A. von Haller (1708–77), H. von Helmholtz (1821–94), C. Ludwig, (1816–18), and C. Bernard (1813–78) had all performed experiments on living organisms. Thompson's method was somewhat different: he would attempt to simulate some biological structure by purely physical means, not to measure the forces actually present in the living organism. By this method:

> we indeed prove what it is the main object of this book to illustrate, namely, that the physical forces are capable of producing particular organic forms. But it is by no means always that we can feel perfectly assured that the physical forces which we deal with in our experiment are identical with, and not merely analogous to, the physical forces which, at work in nature, are bringing about the result which we have succeeded in imitating (pp. 415–416).

Thompson questioned the widely-held assumption that most—if not all—aspects of morphology were best explained by the interplay of heredity and functional adaptation. Thompson's criticisms of contemporary morphologists were rooted in a carefully thought-out philosophy of science.

Thompson's Philosophy of Science

Thompson's father, "D'Arcy the Elder," had taught classics at the Edinburgh Academy. The younger D'Arcy Thompson was himself elected President of the Classical Association in 1929—a unique distinction for a twentieth-century scientist[4]. It is thus not surprising that Thompson's views on morphology were heavily influenced by Plato's geometric idealism and Aristotle's theory of cause. The Platonic influence permeates *On Growth and Form*:

> Cell and tissue, shell and bone, leaf and flower, are so many portions of matter, and it is in obedience to the laws of physics that their forms have been moved, moulded, and conformed. They are no exception to the rule[5] that Θεὸς ἀεὶ γεωμετρεῖ. Their problems of form are in the first instance mathematical problems (p. 8).

And by "mathematical problems" Thompson nearly always meant *geometrical* problems. Thompson's book is filled with examples of how the shapes of living organisms resemble certain mathematical

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[4]When Thompson was awarded an honorary degree at Oxford, the University Orator devoted most of his remarks—delivered in Latin, of course—to praising Thompson's classical scholarship. Only at the end, saying, "but I see the scientists are rising in their seats . . .you claim him for *your* side?" did he turn to Thompson's scientific work.

[5]This aphorism, which Plutarch (*Symposium* VIII, 2) had attributed to Plato, is most often translated as "God is a Geometer." The literal meaning is closer to "God is always geometrizing," or "God always does geometry," but these literal translations are not very good English. Thompson's use of the original Greek is entirely typical.

constructions, such as spirals, polygons, polyhedra, and various forms generated by soap bubbles and soap films. Thompson was particularly struck by the sheer beauty of mathematical regularity:

> For the harmony of the world is made manifest in Form and Number, and the heart and soul and all the poetry of Natural Philosophy are embodied in the concept of mathematical beauty. . .a greater than Milton[6] had magnified the theme and glorified Him "who sitteth upon the circle of the earth," saying: He measureth the waters in the hollow of his hand, he meteth out the heavens with his span, he comprehendeth the dust of the earth in a measure. Moreover, the perfection of mathematical beauty is such (as Maclaurin learned of the bee), that whatsoever is most beautiful and regular is also found to be most useful and excellent. (pp. 778–779)

Thompson was most likely an agnostic when he wrote this passage—the biography written by his daughter (Thompson, 1958) contains a rather unconvincing attempt to demonstrate that her father had, in later years, returned to the faith of his childhood—but his God was most assuredly a geometer.

The introductory chapter gives Aristotle pride of place. "In Aristotle's parable," Thompson remarked, "the house is there that men may live in it; but it is also there because the builders have laid one stone upon another" (p. 5). That is, Aristotle insisted that there was more than one "cause" for the existence of a house—or of an organism. The introductory chapter of *On Growth and Form* is mainly about the different causes for natural forms that morphologists should consider.

For Aristotle, a "cause" of a phenomenon was a *sine qua non*, a

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[6]"A greater than Milton" is a reference to the prophet Isaiah; the passages that follow are paraphrases from the King James translation of Is. 40:22 and Is. 40:12.

condition without which it would not exist. Aristotle had used the example of a house to show that there were four such "causes": the *material cause* was the substance from which it had been built; the *formal cause* was the architect's plan according to which it had been built; the *efficient cause* was the process by which it had been built; and the *final cause* (Greek τέλος) was the purpose for which it had been built—to provide the owner with a new home. Since the absence of any one of these would mean the absence of a house, or at least the absence of this particular house, a complete answer to the question "why does *this* house exist?" must address them all.

In Thompson's view, most contemporary morphologists devoted themselves to the study of formal and final causes while neglecting efficient and material causes.

Contemporary Overemphasis on Heredity

Thompson had two main critisms of contemporary morphologists. First, he felt that many of them were over-eager to invoke shared inheritance as an easy way to explain almost any similarity between two species:

> Although I have tried throughout this book to lay emphasis on the direct action of causes other than heredity, in short to circumscribe the employment of the latter as a working hypothesis in morphology, there can still be no question whatsoever but that heredity is a vastly important as well as a mysterious thing; it is *one* of the great factors in biology. . .but I maintain that it is no less an exaggeration if we tend to neglect these direct physical and mechanical modes of causation altogether, and to see in the characters of a bone merely the results of variation and of heredity, and to trust, in consequence, to those characters as a sure and certain and unquestioned guide to affinity and phylogeny (p. 715).

Stephen Jay Gould has noted that "timelessness is indeed part of the man—as when. . .he rejects the contingency of genealogy, and speaks of geometric permanence, unaltered by mere time" (Gould, 1992:xii). This is not to say that Thompson denied the general truth of evolutionism or the value of homology (*sensu* Owen or *sensu* Darwin) as a morphological concept; what he questioned was the *uncritical* acceptance of appeals to heredity as a mode of explanation:

> The theorem of Organic Evolution is one thing; the problem of deciphering the lines of evolution, the order of phylogeny, the degrees of relationship and consanguinity, is quite another. Among the higher organisms we arrive at conclusions regarding these things by weighing much circumstantial evidence, by dealing with the resultant of many variations, and by considering the probability or improbability of many coincidences of cause and effect; but even then our conclusions are at best uncertain (p. 610).

In keeping with his tendency to question the importance his contemporaries attached to heredity, Thompson was especially skeptical of Mendelian genetics:

> But if we speak, as Weissman and others speak, of an "hereditary *substance*," a substance which is split off from the parent-body, and which hands on to the new generation the characteristics of the old, we can only justify our mode of speech by the assumption that that particular portion of matter is the essential vehicle of a particular charge or distribution of energy, in which is involved the capability of producing motion, or of doing "work." For, as Newton said, to tell us that a thing "is endowed with an occult specific quality. . .tells us nothing (p. 158).

Even in 1917 this was rather a heterodox view. Still more remarkable is the fact that Thompson retained the passage in his second edition, adding in a footnote that a modern biologist, instead of ascribing a "dormitive property" to opium, would "substitute for this occult quality the hypothetical substance *dormitin*" (Thompson, 1942:288).

Contemporary Overemphasis on Teleology

Thompson's second main criticism of contemporary morphologists was concerned with what he saw as overly teleological evolutionary theories. In Thompson's view, while Darwinian natural selection might have abolished divine design from morphology, it remained "a teleology without a τέλος" (p. 4). It provided little more in the way of mechanistic explanations for the growth and form of an organism than had the old natural theology:

> To buttress the theory of natural selection the same instances of "adaptation" (and many more) are used, which in an earlier but not distant age testified to the wisdom of the Creator and revealed to simple piety the high purpose of God. In the words of a certain learned theologian[7], "the free use of final causes to explain what seems obscure was temptingly easy....This method lent itself with dangerous facility to the well-meant endeavors of the older theologians to expound and emphasize the beneficence of the divine purpose." *Mutatis mutandis*, the passage carries its plain message to the naturalist. (P. 672).

"Time out of mind," Thompson noted, "it has been by way of the 'final cause,' by the teleological concept of 'end,' of 'purpose,' or of 'design,' that men have been chiefly wont to explain" (p. 3)

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[7]In a footnote, Thompson gave the source of this passage as "Principal Galloway, *Philosophy of Religion*, p. 344, 1914."

biological adaptation, and "it will be so while men have eyes to see and ears to hear." Thompson did not reject teleological explanations out of hand; unlike Pettigrew he seemed never to take an uncompromising position on any issue. He did feel that an overemphasis on teleology had probably led morphologists to neglect other modes of causation. "When philosophy bids us hearken and obey the lessons both of mechanical and of teleological interpretation, the precept is hard to follow" (p. 5).

"The road of physico-mathematical or dynamical investigation in morphology has had few to follow it," Thompson noted, "but the pathway is old" (p. 8). Along with his analyses of form, Thompson included extensive historical accounts of each morphological and mathematical idea he described. Thompson's historical surveys are comprehensive indeed; in my own historical research I have found very few substantial works on mathematical morphology that Thompson failed to cite. The main conclusion Thompson drew from his scholarly research into the history of mathematical morphology was that much remained to be done:

> we need not wonder if the way be hard to follow, and if these wayfarers have yet gathered little. A harvest has been reaped by others, and the gleaning of the grapes is slow[8]. It behooves us to remember that in physics it has taken great men to discover simple things (p. 8).

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[8]The harvest truly *is* plenteous, but the laborers *are* few; pray ye therefore the Lord of the harvest, that He will send forth laborers into His harvest (Matt. 9:37–38, KJV).

Heredity & Adaptation* vs *Physicalism

Thompson's preferred alternative to heredity and adaptation as an explanatory basis for most aspects of morphology was the *direct* effect of physical forces on the forms of organisms. In his view, only after showing that a given phenomenon could not be explained by ordinary physical laws was the naturalist justified in postulating such special 'biological' modes of explanation as heredity or adaptation. For instance, after showing how soap bubbles often formed structures very similar to those of the earliest stages of embryonic development, suggesting that similar mechanical forces might account for both biotic and abiotic forms, Thompson argued that these similarities cast doubt on the value of phylogenetic inferences drawn from embryological data:

> When we attempt to separate our purely morphological or "purely embryological" studies from physiological and physical investigations, we tend *ipso facto* to regard each particular structure and configuration as an attribute, or a particular "character," of this or that particular organism. From this assumption we are apt to go on . . . to apply our embryological knowledge mainly, and at times exclusively, to the study of *phylogeny.* When we find, as we are not long of finding, that our phylogenetic hypotheses, as drawn from embryology, become complex and unwieldy, we are nevertheless reluctant to admit that the whole method, with its fundamental postulates, is at fault. And yet nothing short of this would seem to be the case, as regards the earlier phases at least of embryonic development (P. 196).

Although Thompson strongly preferred physical explanations, he did not deny that life might turn out to elude physical and mathematical laws; since so many biological phenomena could not yet be explained on the basis of physical laws, the validity of the physicist's approach to biology was as yet untested:

> The appropriate and legitimate postulate of the physicist, in approaching the physical problems of the body, is that with these physical phenomena no alien influence intervenes. But this postulate, though it is certainly legitimate, and though it is the proper and necessary prelude to scientific inquiry, may some day be proven untrue; and its disproof will not be to the physicist's confusion, but will come as his reward...it is in no spirit of arrogant assertiveness that the physicist begins his argument (p. 10).

Thompson's Applications of Physics & Mathematics to Morphology

Because the direct action of physical forces imposed on organisms by their environments played such a major role in Thompson's theory of form, most of his book was organized around the principle of scaling: that the relative magnitudes of different physical forces impinging on any object are very strongly dependent on its size.

Chapter Two of *On Growth and Form* is both an elegant introduction to scaling theory and a general plan for much of the book[9], which begins with accounts of microscopic structures and proceeds to consideration of larger and larger ones. Frequently two species that were widely separated taxonomically but were about the same size would resemble one another more than either species resembled closer, but much larger or smaller, relatives. By devoting each chapter to examples covering a wide taxonomic range but a narrow size range, Thompson accentuated the biological importance of the ways in which physical phenomena scaled with size.

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[9]Spirals represent the most important exception to this generalization. My account of how Thompson explained natural spirals will be deferred to the next chapter.

Scaling: the Consequences of Being a Particular Size

In order to understand how any structure—biotic or abiotic—interacts with its physical environment, one must first know how big it is. Any engineer understands, or quickly learns the hard way, a basic principle that Thompson credited Galileo with discovering:

> neither can a man build a house nor can nature construct an animal beyond a certain size, while retaining the same proportions and employing the same materials as sufficed in the case of the smaller structure[10] (p. 19).

This principle, which Thompson called the "principle of similitude," and modern writers call "scaling," has geometrical, physical, and biological aspects.

The basic mathematical principle is known as the "square-cube law": if two objects are similar in shape but different in size, then the ratio of their areas (of their surfaces and of their cross-sections) will be as the *square* of the ratio of their linear dimensions, but the ratio of their volumes will be as the *cube* of the ratio of their linear dimensions; thus as size increases, volumes increase much faster than areas. "From these elementary principles a great number of consequences follow, all more or less interesting, and some of them of great importance" (p. 16). The dramatic differences in surface to volume ratios between organisms of different sizes have important physical implications:

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[10]Thompson's footnote: "So Werner remarked that Michael Angelo and Bramanti could not have built of gypsum in Paris on the scale they built of travertin in Rome."

> Of the different physical forces, some act either directly at the surface of a body, or otherwise in *proportion* to the area[11] of surface; and others, such as gravity, act on all particles, internal and external alike, and exert a force which is proportional to the mass, and so usually the volume, of the body (p. 16).

Large organisms, such as most vertebrates, have such large ratios of volume[12] to surface area that such "body forces" as gravity, momentum, and kinetic energy are the primary loads on their structures. At small scales, the exact opposite is true: surface area per unit volume is very large, so such phenomena as surface tension, diffusion, and viscous drag are much more important.

Since our intuitions are conditioned by macroscopic organisms, only by a conscious effort are human morphologists able to avoid serious errors: "[for small-scale systems,] the predominant factors are no longer those of our scale; we have come to the edge of a world of which we have no experience, and where all our preconceptions must be recast" (Thompson, 1942:77)

Thompson was critical of the many morphologists who neglected scale effects:

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[11]Actually, some surface phenomena—most notably surface tension—have magnitudes proportional not to area but to length. Of course this only strengthens Thompson's main point, since the ratio of length to volume decreases even more rapidly with increasing size than does the ratio of area to volume. A fly is in mortal peril every time it goes near a drop of water but need not fear gravity; on the other hand, as Vogel (1988:6) remarks, "the fall of an elephant is a matter of the utmost gravity."

[12]At about this point in the second edition, Thompson added the following footnote, which is not present in the first edition: "In the early days of the theory of gravitation, it was deemed especially remarkable that the action of gravity 'is proportional to the quantity of solid matter in bodies, and not to their surface as is usual in mechanical causes; this power, therefore, seems to surpass mere mechanism' (Colin Maclaurin, on *Sir Isaac Newton's Philosophical Discoveries,* IV, 9)" (Thompson, 1942:25).

> We are apt, and even accustomed, to think that magnitude is so purely relative that differences of magnitude make no other or more essential difference; that Lilliput and Brobdingnag[13] are all alike, according as we look at them through one end of the glass or the other. But this is by no means so, for *scale* has a very marked effect on physical phenomena (p. 17).

Because so many aspects of morphology depend upon the physical forces acting on an organism's body, any attempt to understand organic form from a physical and mathematical viewpoint must take into account the vastly different physical circumstances encountered by organisms of different sizes. As Thompson repeatedly emphasized, Lilliput and Brobdingnag *are* different.

Morphology at Small Scales. Chapters IV through IX of *On Growth and Form* are mainly devoted to small-scale aspects of geometrical morphology—cells and tissues. Thompson saw histology and cytology of his day as largely devoted to describing and naming structures, but "to the multitude of visible structures it has often been easier to attribute virtues than to ascribe intelligible functions or modes of action" (pp. 156–157).

Thompson began his account of functional morphology at small scales with a detailed description (taken mostly from E. B. Wilson's classic work) of mitosis and meiosis. He then considered the many mechanical models of these basic processes that had been proposed by previous workers. None of them sufficed to explain all the phenomena, but each could account for some aspects of mitosis and

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[13]In Swift's satirical fantasy, Gulliver was as small, compared to the people of Brobdingnag, as the people of Lilliput were small, compared to Gulliver.

meiosis. Thompson therefore concluded that even though the *actual* forces behind these phenomena remained unknown, the partial success of some models lent support to the idea that a purely physical explanation of mitosis and meiosis might some day be possible. In any case, until mechanical explanations had been ruled out, Thompson was reluctant to accept the need for any type of vitalism[14].

Thompson then considered the forms of cells and tissues from a mathematical and physical viewpoint. As noted above, surface phenomena would be expected to dominate at such small sizes. Thompson's account of cell morphology contains over a hundred diagrams showing how the forms produced by soap bubbles, and by soap films on wire armatures, often resemble the forms of cells. He made particularly extensive use of the mathematical results and the physiological discoveries reported by the Plateaus[15]. As with other cases where physical and mathematical models seemed to provide plausible explanations for morphology, Thompson was critical of contemporaries who favored "biological" explanations. For instance, after showing how the outer "membraneous cups" of certain polyps resemble elastic bags filled with water, Thompson remarked:

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[14]Only long after Thompson's death would electron microscopes reveal the existence of the *cytoskeleton*, a complex network of fibers that are now thought to be the main driving force behind many cellular movements. Even today cytologists can scarcely provide a complete physical model of how mitosis and meiosis work, but it seems certain such an explanation must take into account a whole level of cellular structure below what can be seen in optical microscopes, the very existence of which Thompson and his contemporaries could hardly have suspected.

> Here we have an excellent illustration of the contrast between the different ways in which such a structure may be regarded and interpreted. The teleological explanation is that it is developed for the sake of protection, as a domicile and shelter for the little organism within. The mechanical explanation of the physicist (seeking only after the "efficient," and not the "final" cause) is that it is present, and has its actual conformation, by means of certain chemico-physical conditions; that it was inevitable, under the given conditions (p. 248–249).

From individual cells, Thompson moved on to tissues, which contained large numbers of cells clumped together. Surface tension forces still loomed large in Thompson's models, but now interactions between cells had also to be considered. Even more important, since the cells in a tissue divided up three-dimensional space among them, the geometrical aspects of such a division had to be considered. As Thompson showed, many of these geometrical considerations applied to morphological phenomena at various scales. I shall return to this point later.

Morphology at Large Scales. Chapters XV and V are primarily concerned with physical aspects of morphology at large scales, especially in terrestrial vertebrates. In Thompson's opinion

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[15] *Two* 19th-century scientists named Plateau studied the surface tension phenomena of interest to Thompson: Felix Auguste Joseph Plateau (1841–1911) and Joseph Antoine Ferdinand Plateau (1801–1883). References in the secondary literature to these authors have become hopelessly confused; I even found one library catalog (name omitted to protect the guilty) that listed "Plateau, Joseph Felix (1841–1883)" as the author of works by both. Felix was a naturalist and physiologist who was particularly interested in the biological consequences of surface tension; Joseph was a physicist whose book on fluid statics was for a long time the standard account of surface tension from a physical and mathematical standpoint. The mathematical "problem of Plateau" was stated by Joseph, not by Felix. Thompson generally cited both men as just "Plateau" without any given names. Only by looking in the index to *On Growth and Form*, where there are separate entries for each Plateau, is it possible to determine which one is being referred to in a particular case. In the abridged edition of *On Growth and Form*, prepared by J.T. Bonner (Thompson, 1961), all references to either Plateau are listed in the index under "Plateau, F."

morphologists who studied large organisms had been somewhat more conscious than cytologists and histologists of how physical forces affected natural structures: "Certain problems of this class are by no means neglected by writers on anatomy, and many have been handed down by [the 17th-century anatomist Giovanni Alfonso] Borelli" (p. 690). This was probably because morphologists, being themselves large vertebrates, had direct experience of the physical forces—especially gravity—that predominated at large scales.

In the case of mechanical loads on a skeleton, Thompson did concede the importance of functional adaptation (which, as we have seen, he was often reluctant to concede). Here, he thought, were "many cases where *adaptation,* in the strictest sense, is obviously present, in the clearly demonstrable form of mechanical fitness" (p. 670). Here, he felt, "we are above the region of mere hypothesis, for we have to deal with questions of mechanical efficiency where statical and dynamical considerations can be applied and established in detail" (p. 673). For Thompson, adaptation meant good functional design, in the engineer's sense, but not a Designer! For a structure that must sustain forces due to its own weight—be it a bridge or a skeleton (an analogy Thompson explictly invoked many times)—the primary desideratum of efficient construction is the separation of flexible and rigid members.

Fibers are very efficient at supporting tensile loads, but cannot sustain other types of loading, such as compression, bending,

and shear. In both bridges and skeletons we see a basic division into rigid members (bones or beams) versus tensile members (cables, muscles, tendons, or ligaments). "In preparing or 'macerating' a skeleton, the naturalist nowadays carries on the process till nothing is left but the whitened bones," Thompson complained. "But the old anatomists, whose object was not the study of 'comparative anatomy'. . .were wont to macerate by easy stages; and in many of their most instructive preparations the ligaments were intentionally left in connection with the bones" (Thompson, 1942:968).

There is one basic difference between bridges and skeletons: unlike the beams and cables used by human engineers, the elements of skeletons are themselves very complex structures with their own adaptive responses to loads. Thompson was particularly fascinated by the ways in which muscles, bones, tendons, and ligaments tended to become larger and stronger in response to applied loads. Internal details also responded to changes in mechanical stress patterns. Thompson saw this reconfiguration in response to loads as an example of how biological form was directly molded by external forces:

> It is safe to say that "heredity" need not and cannot be invoked to account for the configuration and arrangement of the trabeculae[16]: for we can see them, at any time of life, in the making, under the direct action of and control of the forces to which the system is exposed (p. 687).

For instance, the trabeculae within a broken and badly reset bone

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[16]Most bones contain numerous small, connected passages filled with fluid. The solid portions of bone between these passages are known as *trabeculae*. Thompson here refers to the fact that trabeculae tend to follow the lines of principal stress within the bone.

will soon reconfigure themselves in alignment with the principal stresses created by the new configuration. Muscles and connective tissue respond in similar ways to applied loads.

Growth, Development, & Evolution as Continuous Transformations

The principles of scaling apply to bridges and organisms alike. However, bridges can be supported by scaffolding[17] while they are under construction; organisms must sustain various loads throughout their growth and development. For this reason Thompson was critical of Darwin's assumption "that it is with nature as with the fancier, who does not care what his pigeons look like in the embryo, so long as the full-grown bird possesses the desired qualities" (p. 58).

After considering the morphological consequences of being a particular size, Thompson went on to consider how size and shape changed with time—developmental time and evolutionary time.

Growth: Change in Size. When the total size—mass or body length—of an organism is plotted as a function of time on graph paper, one striking trend is evident in many species: growth is usually very rapid in early life, but declines with age, and may even reverse itself in old age. To emphasize this trend, Thompson

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[17]When I was an engineering student, I learned that most structural failures take place during construction precisely because human structures-in-progress cannot support themselves without scaffolding—and scaffolding, as a temporary structure, is generally designed and built with far less care than is the permanent structure.

also plotted the first and second derivative of the function connecting size with time—giving the rate of growth, and what he termed the "acceleration" of growth, in obvious analogy to Newtonian methods for studying how a particle moves under the influence of gravity. Thompson placed particular stress on the time during the growth of a mammal when the acceleration becomes negative; mathematically this is known as the "inflection point" of the growth curve. However, if the growth curve is plotted on a different type of graph paper (most often using a logarithmic scale), then this inflection point is no longer seen. Many of Thompson's contemporaries, and most of his successors, considered the use of logarithmic plots more physiologically reasonable. Thompson disagreed:

> It was apparently from a feeling that the velocity of growth ought in some way to be equated with the mass of the growing organism that Minot introduced a curious, and (as it seems to me) an unhappy method of representing growth, in the form of what he called "percentage curves"; a method which has been followed by a number of other writers and experimenters. Minot's method was to deal, not with the actual increments added in successive periods, such as years or days, but with these increments represented as *percentages* of the amount which had been reached at the end of the former period. . .[which is] tantamount to plotting log y against x, that is to say, the logarithm of the size against the time. This could only be defended and justified if it led to some simple result, for instance if it gave us a straight line (pp. 72–73).

That is, if we plot size as a function of time on logarithmic graph paper, then only exponential growth will produce a straight line. On a linear plot such as Thompson preferred, the slope of the curve at a given time is proportional to $\frac{dy}{dt}$, or the *amount* by which the size changed in one unit of time. On a logarithmic plot such as many others preferred, the slope of the curve at a given point is

proportional to $\frac{dy}{t \cdot dt}$, or the *ratio* by which the size increased in one unit of time. If biological growth were by compound interest, with each portion of the body always adding the same small fraction to its size, then the plot of size versus time on a logarithmic scale would be a straight line. It rarely is.

I think this divergence from his contemporaries reflected two tendencies in Thompson's thought: he saw biological form as following the same laws as inanimate form, and he sought mathematical simplicity in all things. Since the more complex method of plotting data did not generate a simpler curve, Thompson preferred the simpler method of plotting data.[18] Thompson thought the inflection point on his graphs very important, but was not able to identify any specific physiological or developmental event which coincided with this specific instant in time. Thompson did note that important events in the life-history of an individual were often accompanied by sudden changes in its growth rate. He cited as examples the growth spurts following birth and accompanying puberty in mammals, and the pauses in growth that accompany metamorphosis in amphibians and invertebrates.

Development: Change in Shape. If all parts of an organism were to grow equally fast in all directions, then its form would remain constant while its size alone changed. Of course, from the

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[18]Hutchinson (1948) said of Thompson's preference for plotting growth on a linear scale that "where simplicity conflicts with generality, simplicity, backed by the aesthetics of Greek geometry, wins."

discussion of scaling on page 61, it may be obvious that such a simple size increase would itself entail a change in mechanical function. Moreover, morphology presents few examples of isolated size increase. Thompson saw development as largely a process of non-uniform growth.

In most mammalian species, the head, trunk, and internal organs grow much more slowly than does the body as a whole:

> None of these organs by any means keeps pace with the body as a whole in regard to growth in weight; in other words there must be some other part[19] of the fabric, doubtless the muscles and the bones, which increase *more* rapidly than the average increase of the body (p. 89).

The limbs, on the other hand, grow much more rapidly than does the rest of the body. Many of the differences between a child and an adult result from just such differential growth rates.

Thompson noted similar patterns, varying only in their details, in other animal species and in plants. Uniform growth of all parts at once is extremely rare in the living world. Therefore "the form of an organism is determined by its rate of growth in various directions" (p. 52). The embryo becomes an adult by a continuous transformation, rather than by mere enlargement.

Evolution: Change in Species. The longest time scale over which Thompson studied biological transformations was the evolutionary time scale. As with the other processes by which

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[19]The passage appears thus in the first edition; in the second edition Thompson corrected the sentence to read ". . .other parts. . ."

biological forms changed over time, evolution had generally involved changes in the *relative sizes of corresponding parts*; completely novel structures were quite rare. These changes in proportions ultimately reflected differences in relative growth rates throughout the life of each individual organism in a lineage. Homologies could be identified precisely because the evolutionary and developmental transformations involved had been gradual, continuous, and structure-preserving.

Thompson saw all tranformations of form as an interaction of still-mysterious hereditary tendencies with external physical forces:

> The deep-seated rhythms of growth which, as I venture to think, are the chief basis of morphological heredity, bring about similarities of form, which endure in the absence of conflicting forces; but a new system of forces, introduced by altered environments and habits. . .will assuredly not be long of manifesting itself in notable and inevitable modifications of form [so that] modifications of form will tend to manifest themselves, not so much in small and isolated phenomena. . .but rather in some slow, *general,* and more or less uniform or graded modification (pp. 717–718).

It is this view of evolutionary change which I believe is at the root of what so many modern commentators consider Thompson's most original contribution to morphology: the method of coordinate transformations. Thompson's method of studying the evolution of complex forms focused on the *changes* rather than on the forms themselves.

In many cases, two complex forms can be related by a simple transformation. For example, a flat map of the world and a globe are both complex shapes, but the relationship between them is

simple: "The problem is closely akin to that of the cartographer who transfers identical data to one projection or another" (p. 724) except that, despite the similarities of mathematical technique:

> The morphologist will not seek to draw his organic forms in a new and artificial projection; but in the converse aspect of the problem, he will inquire whether two different but more or less obviously related forms can be so analysed and interpreted that each may be shown to be a transformed representation of the other. This once demonstrated, it will be a comparatively easy task (in all probability) to postulate the direction and magnitude of the force capable of effecting the required transformation. Again, if such a simple alteration of the system of forces can be proved adequate to meet the case, we may find ourselves able to dispense with many widely current and more complicated hypotheses of biological causation (p. 724)

To demonstrate this, Thompson drew many figures showing how the shape of one species could be transformed into that of another. Usually, he would draw one species on rectilinear graph paper, then redraw the figure on a second sheet of paper in which curved lines replaced the straight lines of the original graph paper. Frequently a very simple geometrical transformation would make one species look almost identical to another. One major limitation of his method was that it compared the adult form of one species with the adult form of another species, which implied that he saw the evolutionary process as a transformation from adult to adult. However, as his discussions of growth and development clearly show, Thompson was well aware that each adult had developed—by a series of continuous transformations—from an embryo.

Having demonstrated that it was often possible to find simple descriptions of the mathematical relationship between two biological forms, Thompson went on to consider what this might mean in terms of

physical "systems of force" imposed on the organism by its environment:

> We are dealing in this chapter with the forms of related organisms, in order to shew that differences between them are as a general rule simple and symmetrical, and just such as might have been brought about by a slight and simple change in the system of forces to which the living and growing organism was exposed. Mathematically speaking, the phenomenon is identical with one met with by the geologist, when he finds a bed of fossils squeezed or otherwise symmetrically deformed by the pressures to which they, and the strata which contain them, have been subjected. . .but the deformation due to direct vertical pressure in a horizontal stratum is not nearly so striking as are the deformations produced by the oblique or shearing stresses (p. 728).

While Thompson never explicitly stated what forces were in fact present to cause such transformations, he clearly seems to have imagined them as mechanical. A question which Thompson did not address is what would happen if the novel "system of forces" were removed. Would the "rhythms of growth" retain their prior pattern throughout? This would imply that reversion to a prior evolutionary stage should occur if the physical environment returned to a prior state.

I doubt that Thompson actually thought this would happen. Since he generally avoided discussing heredity, it is not clear how he did regard the relation between environmental effects and inherited effects. He accepted natural selection only as a process of winnowing out the failures; he rejected the idea that selection could be a creative factor in evolution. Thompson gave only the barest hint of his own answer: "to discuss these questions at length would be to enter on a discussion of Lamarck's philosophy of

biology, and of many other things besides" (p. 716).

The Geometry of Space: Some Phenomena are not Size-Dependent

Regular arrays of smaller structures are common in morphology, at a wide range of sizes. Thompson used dozens of examples—from such diverse structures as plant parenchyma, vertebrate tissues, dragonfly wing venation, embryonic cleavage, insect nests, coral reefs, tortoise carapaces, and radial septa of medusae (to name but a few)—to show that certain angles were especially common in such arrays. Angles of 90°, 120°, and approximately 109° were nearly ubiquitous, and their arrangements followed certain regular patterns. Inorganic examples of such arrays were also common; among the examples of these noted by Thompson were cracks in drying mud or paint, huge basaltic columns, ice crystals, and soap bubble clusters.

In the case of soap films it was relatively easy to find a physical explanation for such patterns: a straightforward static analysis of the forces present where soap films meet reveals that only certain angles are stable: 90°, 120°, and 109°28′16″ are the only stable possibilities if the soap films are of a uniform composition. Since such similar geometrical patterns spontaneously arose in such diverse physical and biological systems over such a vast range of scales, it seemed unlikely that they all resulted from

the same physical forces. Rather, Thompson contended, they were dictated by the geometry of space itself. In two long, detailed, but strikingly lucid chapters, Thompson showed how a vast number of polyhedral arrays could be reduced to a small number of geometrical configurations.

These basic configurations, in turn, could be explained by a few geometrical assumptions; while these assumptions were analogous to those required to explain the forms of soap bubbles they clearly had much wider application. From this analysis, Thompson drew his usual conclusion: that the vast range of natural structures exhibiting such forms could be explained by very simple geometrical laws, and therefore neither heredity nor adaptation need be invoked. For instance, Thompson showed that eight bubbles of approximately the same size could only form thirteen stable arrangements. Every one of these arrangements, and no others, could actually be found in the best embryological descriptions. Thus, Thompson concluded:

> We now begin to realise the remarkable fact, which may even appear a startling one to the biologist, that all possible groupings or arrangements whatsoever of eight cells. . .are referable to some one or other of *thirteen* types or forms. And that all the thousands and thousands of drawings which diligent observers have made of such eight-celled structures, animal or vegetable, anatomical, histological, or embryological, are one and all representations of one or another of these thirteen types (p. 383).

The same basic geometrical rules applied also to honeycombs, Thompson noted. The old natural theologians—and Pettigrew—had adduced honeycombs as excellent examples of God's "design"; Charles Darwin devoted a dozen pages of his *Origin* (Darwin, 1859:224–235) to an attempt at explaining the regularity of honeycomb cells as the

result of natural selection. Despite the differences in their explanations, both Darwin and the natural theologians accepted the idea that the honeycomb was to be explained primarily on functional grounds.

Thompson had several criticisms of the assumption that honeycomb structure represented a functional adaptation. First, he pointed out that the geometry involved resembled that of the tissues and soap bubble arrays discussed above; therefore, he concluded:

> That the beautiful regularity of the bee's architecture is due to some automatic play of the physical forces, and that it were fantastic to assume (with Pappus and Réamur) that the bee intentionally seeks for a method of economising wax, is certain, but the precise manner of this automatic action is not so clear (p.331).

Second, he questioned whether the pattern was so regular as had been generally assumed. Many authors, he believed, had confused theoretical calculations of ideal angles with actual measurements, and "nobody appears to have thought of the impossibility of measuring such a thing as the end of a bee's cell to the nearest minute" (p. 330). Finally he pointed out that the difference in wax consumption between the supposedly optimal configuration and a number of other shapes was in fact negligible. Nineteenth-century analyses of honeycomb geometry made much of the "cap" at the end of each cell: the cell is not a simple hexagonal tube with a flat end, but has a little pyramid at its end. This shape—a hexagonal tube capped with a pyramid—is very close to the ideal shape that would use the minimum possible amount of wax.

Thompson calculated the amount of wax used per unit volume of honey stored in an ideal cell, and in one with a flat end. The difference was about 2 percent; since variations in wall thickness were much greater than this, Thompson concluded that the end cap did not in fact provide any functional advantage. On this basis, Thompson concluded that the honeycomb, like many other aspects of biological form, was generated by physics and mathematics, not by adaptation.

I said earlier in this chapter that I was deferring Thompson's analysis of spiral structures to the next chapter. As we shall see, spirals are another prominent example of size-independent and taxon-independent geometrical morphology. Not surprisingly, Pettigrew considered the striking similarities of diverse natural spirals proof of Divine Design; Thompson would rather invent mathematical hypotheses than Divine Designers.

CHAPTER 5

Pettigrew and Thompson on Spirals

Perhaps the contrasting approaches to organic form represented by Pettigrew's *Design in Nature* and Thompson's *On Growth and Form* can be put into sharpest focus by considering a specific topic to which both authors devoted considerable attention. Pettigrew and Thompson were clearly fascinated by the numerous spirals found in the living world. In many ways, their treatments of spirality[1] exemplify the similarities and differences in their basic approaches to organic form. As we saw in Chapter Three, Pettigrew favored the divine-design hypothesis of natural theology as explanatory of a number of morphological facts that he thought were inconsistent with contemporary evolutionary theories. His view of spirals, as of other aspects of morphology, was purely descriptive, making no use of mathematical analyses or physical models. On the other hand, Thompson (as we saw in Chapter Four) sought mathematical descriptions and physical models of the processes of growth and development that had produced organic forms. He saw contemporary morphologists as attempting to explain virtually all aspects of morphology in terms of history or teleology, neglecting those aspects of morphology that could be more profitably studied by the use of mathematics and physics.

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[1] I am borrowing the word "spirality" from the American biologist Raymond Pearl, who used it in his review of *Design in Nature* (Pearl, 1909).

I. Pettigrew's Treatment of Spirals

Spirals are a major theme of Pettigrew's *Design in Nature*, to which the book returns again and again. Nearly one third of the 457 numbered sections into which Pettigrew divided his book make at least brief mention of spirals. Even the subtitle of the book begins with the words: "As Illustrated by Spiral and Other Arrangements. . ." (Pettigrew, 1908:v). The sections dealing with spirals are not confined to one portion of the work; descriptions of spirals appear in many different places.

A. Diversity of Natural Spirals

Pettigrew used more than a hundred drawings and photographs to show that spirals are found throughout the natural world ("inorganic and organic Kingdoms" is his often-repeated phrase). Examples from the "inorganic Kingdom" that are discussed in Pettigrew's three volumes include astronomical bodies (such as the Great Nebula in Andromeda[2]), atmospheric phenomena (such as tornados and sandstorms), and certain crystals. Such examples were intended to show the "prevalence of spiral arrangements on a grand scale in the physical universe" (Pettigrew, 1908:10). Pettigrew speculated that the very nature of matter must be fundamentally spiral, since

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[2]Today known as the Andromeda *Galaxy*. In Pettigrew's day, the existence of galaxies beyond our own was not yet suspected. Pettigrew mentioned a contemporary estimate of five light years for the diameter of the Great Nebula in Andromeda; modern estimates are roughly 24,000 times that turn-of-the-century figure.

> According to the electrical theory of matter, the sub-atoms, corpuscles, or electrons are subject to various kinds of strain, are in a constant state of excitement, and in a perpetual whirl of movement, spiral or otherwise; the movements being as important as the matter moving. The electric theory of matter, it will be observed, puts spiral and other movements in the forefront of cosmic arrangements (Pettigrew, 1908:12).

However, Pettigrew never made it clear what he thought the causal connections among his various inorganic spirals might be. He did seem to believe that something beyond known physical laws was needed to explain the prevalence of spirals in nature:

> Some will no doubt endeavor to explain the marvellous spiral arrangements witnessed in nebulae by attractions and repulsions of various kinds; they will regard the phenomenon as of purely physical origin. Such an explanation. . .would be inadequate to explain similar spiral arrangements occurring in plants and animals (Pettigrew, 1908:14)

The biogenic[3] spirals discussed in Pettigrew's three volumes are even more numerous, and far more diverse, than the non-biogenic spirals. Pettigrew presented scores of examples from throughout the plant and animal kingdoms, a few of which I have reproduced as Figures 1–3. Among his zoological examples are molluscan shells; foraminiferal tests; and vertebrate teeth, tusks, horns, and claws. Many plant structures, including palm trees, daisies, pineapples, and pine cones, are composed of smaller units in a spiral array; these are also discussed. Pettigrew also mentioned the complex arrangements of fibers found in plant stems, blood vessel walls, and many vertebrate organs, such as the heart and the digestive tract.

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[3] I am using the word "biogenic" because many of the spirals found in morphology consist of *non*-living material that has been laid down by *living* organisms. For instance, a snail shell, made of inorganic material, cannot accurately be described as either "organic" or "inorganic": it is an inorganic object of biogenic origin.

Pettigrew adduced what he called "the electrical theory of matter" as proof that whirling movements were fundamental to all matter; he saw this as proof that spirality was a basic feature of the universe. Living matter of course partook of the spirality that pervaded the universe, but living matter had an additional fundamental characteristic not found in the abiotic universe: chirality, or molecular asymmetry. Like Japp (whose famous lecture at the British Association meeting of 1898 was one of the main sources cited in Pettigrew's account of stereochemistry) and Pasteur, he regarded chirality as a fundamental difference between organic and inorganic chemistry, because no purely physical method of producing an optically active solution had ever been found. As Pettigrew summed-up Japp's views: "Non-living, symmetric forces, therefore, acting on symmetric atoms or molecules, cannot produce asymmetry" (Pettigrew, 1908:19). Only the actions of an intelligent designer could have created the asymmetry of life *ex nihilo*. Pettigrew was not alone in his contention that stereoisomerism proved chemistry and physics alone could not account for life. However, to this vitalistic conclusion Pettigrew added his own unique twist: the asymmetric, "twisted," arrangement of the atoms making up living molecules proved that spirality was even more characteristic of the living world than of the universe generally. Many organisms had visible spirals; all organisms has invisible spirals as a feature of their basic structures.

The fibers found in the walls of hollow organs had personal, as well as scientific, significance for Pettigrew because his first original research project (as a student of John Goodsir at Edinburgh) had been to determine the arrangement of muscle fibers in the vertebrate heart. After months of work, Pettigrew had been unable to make sense of his many dissections, until one day he hit upon an elegant model:

> A lucky accident came to my assistance. One day I came down to dinner a little earlier than usual, and casually taking up a newspaper commenced to roll it layer upon layer obliquely from one corner as grocers do in making conical paper bags (Pettigrew, 1908:1366).

The lines of type on the newspaper wound around the cone in much the same fashion as the fibers of the heart muscle. Later Pettigrew was to find similar fiber arrangements in the walls of other organs, such as the stomach. All these fiber arrangements Pettigrew included among his examples of biological spirals. Many other biological curves were also included among Pettigrew's examples of spirals.

B. Evolutionists Cannot Explain Spirals

Pettigrew strongly felt that all the spirals he described must have a common cause other than coincidence: "we are forced to look for a cause, and to remove them from the category of chance formations" (Pettigrew, 1908:26). As we saw in Chapter Three, he flatly rejected any form of evolutionary theory. For Pettigrew, homology—*sensu* Owen or *sensu* Darwin—had no biological basis. As

part of his attack on evolution Pettigrew stressed characters (such as spirality) that did not have any evident connection to standard taxonomic theories:

> If radiating, concentric, and spiral structures and movements obtain in plants and animals from the lowest to the highest. . .there is no need and indeed no excuse for saying that a vertebrate animal with a backbone is merely a higher form of an articulate animal, or that the higher vertebrates are the linear [*sic*] descendants of the lower vertebrates" (p. 686).

Pettigrew considered spirals to be positive proof of intelligent design. Spirality, he insisted, was a universal theme in the Creator's design of nature:

> The resemblance between the inorganic and organic nebular spirals and the organic plant and animal spirals is in no sense fanciful. . .if proof were wanting of the intimate relations subsisting between the inorganic and organic kingdoms, and of the unity of plan which pervades all nature, these remarkable coincidences in spiral formations are well calculated to supply it. The inorganic and organic spirals cannot, everything considered, be regarded as chance productions. They undoubtedly owe their origin to a common law, and afford a striking proof of a first cause. . .no marvel, then, if plants and animals assume shapes and movements which are common in the heavenly bodies. Endless examples of spiral structures and spiral movements are given further on (Pettigrew, 1908:14)

> No doubt many will fail to perceive any possible connection between a spiral sand-storm, spiral water-spouts, spiral nebulae, &c., and the spiral stems and revolving movements of plants, and the twisted limbs and spiral movements of animals, as seen in walking, swimming, and flying; and if so, no one will be disposed to cavil or impute blame; still the resemblances are so striking, when carefully looked into, that no scientific inquirer can afford to pass them over. . .they, in fact, point to the existence of a great law of growth, development, and movement which reigns supreme in both [inorganic and organic] kingdoms (Pettigrew, 1908:101).

Pettigrew never described this "law of growth, development, and movement" in any detail. Nor, despite his frequent assertions that spirals represented mathematical perfection, did he make any attempt to describe spirals in mathematical terms. I find Pettigrew's omission of the mathematics of spirals particularly

interesting because his own mentor, John Goodsir, had been so fascinated by the Moseley model of molluscan shell geometry. Goodsir's *Anatomical Memoirs* (1868) contain extensive descriptions and effusive praise for Moseley's (1838) paper on molluscan shell geometry. According to Lonsdale (1868), Goodsir spent the last years of his life seeking geometrical regularities in sundry natural forms. Pettigrew simply asserted that the similarities between these spirals proved the existence of such a law.

II. Thompson's Treatment of Spirals

Like Pettigrew, Thompson was clearly fascinated by spirals. *On Growth and Form* has four chapters (out of seventeen) devoted to the mathematical description of morphological spirals, and other chapters mention spirals in passing. Unlike Pettigrew, Thompson confined nearly everything he had to say about spirals to a group of contiguous Chapters, Ten through Fourteen. Aside from those in one section of Chapter Nine, every other allusion to spirals in Thompson's *On Growth and Form* is very brief.

A. Diversity of Organic Spirals

Thompson used almost exactly the same set of biological examples as had Pettigrew to show that a great many plants and animals, from nearly every major taxonomic group, have spiral forms

or spiral parts. Many of Pettigrew's drawings of morphological spirals could be used to illustrate Thompson's discussions of spirals; many of Thompson's drawings could be used to illustrate Pettigrew's book. Figures 4–6 show a few of Thompson's illustrations; note their similarity to Figures 1–3 (which were taken from Pettigrew's book). Unlike Pettigrew, Thompson focused on morphological spirals. Every spiral mentioned in the first edition of *On Growth and Form* is biogenic. As we saw in Chapter Four, Thompson frequently showed non-biological examples of a particular shape alongside biological examples in order to demonstrate that causes acting in the physical universe may well explain many aspects of biological form. The fact that Thompson made no mention[4] of non-biogenic spirals suggests that in this case he saw a basic difference between forms produced by life and all other forms. I will come back to this point later.

Unlike Pettigrew, Thompson certainly did not see stereochemistry as a fundamental difference between living organisms and inorganic chemistry; nor did he see chirality as being in any way connected to spirality. His brief discussion of chirality—in a chapter that makes no mention of spiral morphology—is a typically scholarly review of a long-standing scientific controversy, summarizing every major viewpoint on the subject. While he considered the origin of molecular asymmetry an open question,

[4]A few very brief references to non-biogenic spirals were added to the second edition (Thompson, 1942) of his book, but none of them were in the first edition.

Thompson found Byk's hypothesis particularly promising: perhaps circularly-polarized light from the sun had selectively degraded molecules of one handedness at an early stage in the origin of life. This theory Thompson saw as "an example limited but yet crucial (*if confirmed*) of an asymmetric force, non-vital in its origin, which might conceivably be the starting-point of that asymmetry which is characteristic of so many organic products" (Thompson, 1917:419). I emphasize that stereochemistry was not central to any of Thompson's major themes, and he did not link it in any way to spirals. Thompson's brief discussion of chirality is mentioned here only because Pettigrew considered it so central to his account of spirality.

B. Difficulties for Darwinism

Like Pettigrew, Thompson saw spirals as an important example of how biological forms did not always fit the approach to evolutionary morphology then popular. However, Thompson diverged from contemporary orthodoxy in a direction very different from that of Pettigrew's design argument. As I explained in Chapter Four, Thompson objected to contemporary Darwinism precisely because he thought it was too similar to the older natural theology, with its focus on homology (revealing God's master plan) and analogy (revealing God's purposeful designs). Contemporary evolutionists had simply substituted reference to shared ancestry (as explanatory

of homology *sensu* Owen) and reference to natural selection (as explanatory of adaptation). In the first place, he thought that many of his contemporaries had exaggerated the importance of homologies. Some structures, Thompson conceded, might well be homologous with one another in the hereditary sense. The spirals found in structures from different taxonomic groups were not:

> Among such forms as these, and the many others which we might easily add to them, it is obvious that we have to do with things which though mathematically similar, are biologically speaking fundamentally different. And not only are they biologically remote, but they are also physically different, in regard to the nature of the forces to which they are severally due (Thompson, 1917:495)

Secondly, he was very skeptical of natural selection as an explanation for many patterns of biological form. Spirals were a prime example of a morphological pattern that did not seem to have resulted from natural selection:

> We find the same forms, or forms which (save for external ornament) are mathematically identical, repeating themselves in all periods of the world's geological history; and, irrespective of climate or local conditions, we see them mixed up, one with another, in the depths and on the shores of every sea. It is hard indeed (to my mind) to see where Natural Selection necessarily enters in, or to admit that it has had any share whatever in the production of these varied conformations (Thompson, 1917:586)

C. Mathematical Models of Spirals

Thompson's attempt to explain biological spirals was quite different from Pettigrew's. First, he drew careful distinctions among the different types of spirals found in the living world; while many could be given elegant mathematical descriptions, some could not; for instance, "a true spiral, though not, by the way, so

easy of investigation, is presented to us by the outline of a cordate leaf" (Thompson, 1917:495). Different types of spirals, Thompson emphasized, might well require different explanations. He chose to focus on those spirals that could be analyzed with the mathematical tools at his disposal. He also placed particular stress, with spirals as with many other aspects of morphology, on the relationship between the present form of an organic structure and the process of growth that had produced it.

In some important respects, Thompson's treatment of spirals was quite different not only from Pettigrew's account of spirals, but also from the rest of his own book. As we saw in Chapter Four, two themes permeate most of *On Growth and Form*: the laws of scaling and the resemblances between living and non-living structures. Neither of these principles is stressed in Thompson's account of spirals. The laws of scaling mean that the forces shaping a foraminiferan (such as *Globigerina*) and a chambered nautilus must be very different:

> It follows from all this there cannot possibly be a physical or dynamical, though there may well be a mathematical *Law of Growth*, which is common to, and which defines, the spiral form in the Nautilus, in the Globigerina, in the ram's horn, and in the disc of the sunflower. (Thompson, 1917:495–496)

That is to say, the strong relationship between size and shape that permeates so much of Thompson's book could not apply to these shapes. As we saw in Chapter Four, Thompson showed that organisms of different sizes were subject to very different physical forces, while organisms of similar sizes were subject to similar physical forces; as a result organisms of different sizes tended to be very

different in shape while organisms of similar sizes were often quite similar. The striking resemblances between spirals of very different sizes suggested that they could not result from the same physical forces.

How, then, could there be a common law governing these diverse spirals? Many, though by no means all, of the biological spirals Thompson examined were very similar to a mathematical curve known as the "logarithmic" or "equiangular" spiral. The mathematical model Thompson used was that of Moseley[5] (1838). The key idea is that every portion of this curve is similar in shape to every other portion. The *Nautilus* shell depicted in Figures 2 and 5 is an excellent example of what I mean.

The starting point from which the curve spirals outwards is known as the *pole* of the spiral. If lines are drawn radiating from the pole, all will intersect the curve at almost exactly the same angle: about 80° (different species have different values of this characteristic angle, but the constant-angle property is found in nearly all spiral shells). Notice how the main spiral of the shell is intersected by a number of curved partitions, known as *septa.* The septa divide the shell into many small segments. Each of these segments is geometrically similar to every other segment; they differ only in size. A photograph of one segment could be enlarged

[5]Recall that Pettigrew's mentor, John Goodsir, had very high praise for Moseley's elegant models; despite this background and Pettigrew's interest in spirals, the three volumes of *Design in Nature* contain no mention whatever of Moseley's work.

or reduced to match a photograph of any other. The property permitting this is known as the "self-similarity" property. Thompson saw this self-similarity property as evidence for a simple law of growth:

> In the growth of a shell, we can conceive of no simpler law than this, namely, that it shall widen and lengthen in the same unvarying proportions: and this simplest of laws is that which Nature tends to follow. The shell, like the creature within it, grows in size *but does not change its shape* (Thompson, 1917:507).

Most natural equiangular spiral structures are composed of rigid, and often non-living, material that has been progressively laid down as the organism grew. That is:

> In the great majority of cases, when we consider an organism in part or whole...we have no reason (or very little) to consider one part of the existing structure as *older* than another; through and through, the newer particles have been merged and commingled, by intussception, among the old; the whole outline, such as it is, is due to forces which are still for the most part at work to shape it, and which in shaping it have shaped it as a whole. But the horn, or the snail-shell, is curiously different; for in each of these, the presently existing structure is, so to speak, partly old and partly new; it has been conformed by succcessive and continuous increments...the same is true of the spirally arranged florets of the sunflower. For here again, we are regarding serially arranged portions of a composite structure, which portions, similar to one another in form, *differ in age,* and they differ also in magnitude in a strict ratio according to their age. Somehow or other, in the logarithmic spiral the *time-element* always enters in (Thompson, 1917:496).

It is such growth by accretion, combined with some very simple geometry, that accounts for these equiangular spirals:

> We simply presuppose that the increments of growth take place at a constant angle to the growing surface...let us also assume that the whole structure is rigid, the new accretions solidifying as they are laid on (Thompson, 1917:500).

If each new addition is added at the same angle to the prior portion, the result will inevitably be the *self-similarity* property which is posessed by all equiangular spirals. Thus, Thompson saw

equiangularity as a mathematical consequence of a very simple growth pattern; he was quite critical of those who ascribed a mystical or vitalistic significance to such curves.

The second main class of biological spirals analyzed by Thompson were the complicated arrays of soft fibers found in the walls of many organs. The reader will recall that Pettigrew had a special interest in these structures because his first important contribution to morphology had been the detailed description of such structures. As with equiangular spirals, Thompson accounted for these arrays of fibers by reference to simple geometry and the characteristics of growth processes. The key geometrical concept can be found in any standard nineteenth-century textbook on solid geometry:

> A geodesic line on a surface is such that every small element *PQ* is the shortest that can be drawn on the surface between *P* and *Q*...in the case of developable surfaces...when the surface is developed, the geodesic must become a straight line. Thus the geodesics on a right circular cylinder are easily seen to be helices. (Aldis, 1886:219–220).

If one stretches a string over a curved surface, the string will tend to follow the geodesics on that surface; for example, a string stretched over a globe will follow the "great circles" that are the shortest possible routes for long air or sea journeys. Similarly, fibers in the wall of an organ will tend to follow geodesics. The geometry was not original with Thompson. However, I think his combination of geodesic theory with the analysis of growth was orginal:

> A very instructive case is furnished by the arrangement of the muscular fibres on the surface of a hollow organ, such as the heart or stomach. Here we may consider the phenomenon from the point of view of mechanical efficiency, as well as from that of purely descriptive or objective anatomy. In fact we have an *a priori* right to expect that the muscular fibres covering such hollow or tubular organs will coincide with geodetic[6] lines. . .the muscular fibres, as they wind over the surface of an organ, arrange themselves automatically in geodesic curves. . .[thus] we see the production of those "figures-of-eight," to which, in the case for instance of the heart-muscles, Pettigrew and other anatomists have ascribed peculiar importance. In the case of both heart and stomach we must look upon these organs as developed from a simple cylindrical tube, after the fashion of the glass-blower (p. 490).

That is, if the organ begins its developmental process as a simple tube (as many organs do), and the fibers in the wall of this tube remain under tension while the organ develops by slow deformation, then these fibers will continue to follow geodesics throughout the developmental transformations. The end result can be very complex, as Pettigrew had demonstrated, but the mechanism was again very simple.

III. Summary

The treatments of spirality found in these two books are in many respects typical of the divergent approaches to organic form that I described in Chapters Three and Four. Neither author's view of natural spirals is at all typical of early twentieth-century morphologists. Both authors saw spirals as examples of what was wrong with contemporary approaches to the study of morphology, and used many of the same examples to show how spirals did not fit well

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[6]In his first edition, Thompson used the older spelling (geodetic) and the newer spelling (geodesic) with roughly equal frequency. In his second edition, most occurences of "geodetic" were changed to "geodesic." In modern usage, "geodetic" generally refers only to measuring the exact shape of the earth.

into standard evolutionary theories. However, despite all the similarities, these two accounts of spirals also illustrate the sharp differences in the explanatory modes preferred by these two authors.

This completes my comparison of Pettigrew's *Design in Nature* and Thompson's *On Growth and Form*. In Chapter Six I will consider what other scientists have said about these two books, at the time of their publication and in later decades.

Figure 1. Cross-section of snail shell, from Pettigrew.

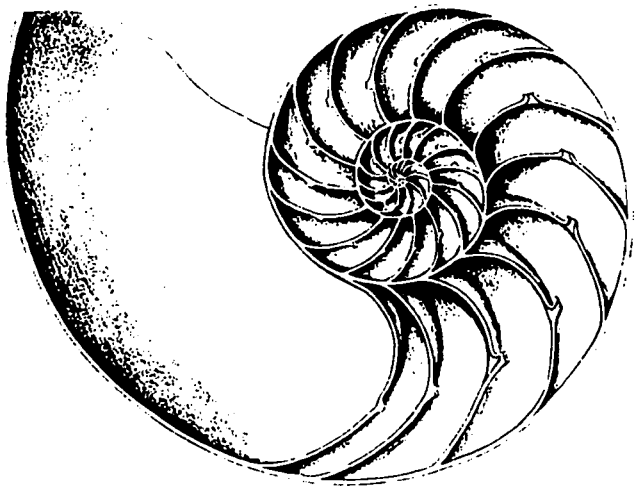

Figure 2. Cross-section of *N. pompilius* shell, from Pettigrew.

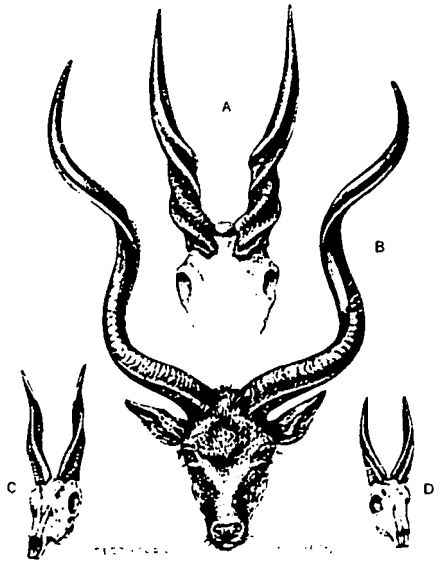

Figure 3. Spiral horns, from Pettigrew.

Figure 4. Cross-Section of snail shell, from Thompson.

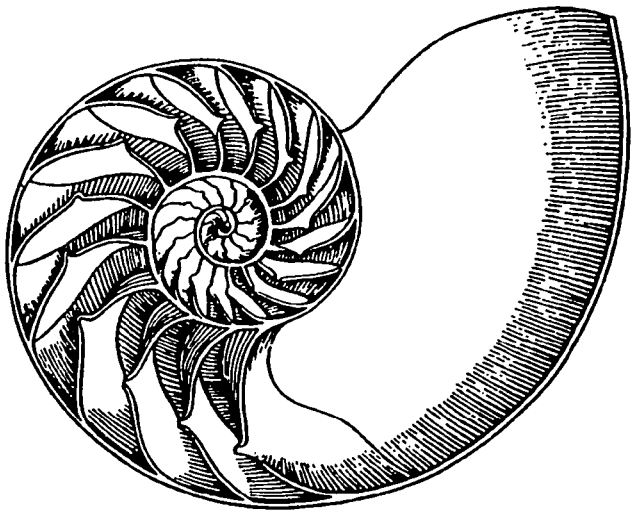

Figure 5. Cross-section of *N. pompilius* shell, from Thompson.

Figure 6. Spiral horns, from Thompson.

CHAPTER 6

Reception of The Two Books

In Chapters Three through Five I described the striking similarities and equally striking differences between Pettigrew's *Design in Nature* (1908) and Thompson's *On Growth and Form* (1st Ed. 1917; 2nd Ed. 1942). In this chapter I will consider critical reactions to the two books—reactions that could hardly have been more divergent. Despite Pettigrew's prominence, contemporary reviews of *Design in Nature* were extremely negative. Thompson was not so well-known when *On Growth and Form* was published, but contemporary reviews were very favorable, and the book remains in print[1] today, widely acknowledged as a classic in its field.

At the time of his death in 1908 Pettigrew had been Chandos Professor of Medicine and Anatomy at St. Andrews, Scotland's oldest university, for 33 years. Before his death he had completed the manuscript of *Design in Nature* and had begun checking the printer's proofs. Pettigrew's reputation as an anatomist assured that his book would be taken seriously by the scientific community (four major periodicals published reviews), but the book was soon forgotten. The only work (so far as I know) to make extensive use of *Design in Nature* as a source was Cook's *The Curves of Life* (1914). Cook's assessment of *Design in Nature* was more favorable to it than was

[1]Cambridge University Press kept the second edition in print from 1942 until the late 1980s; shortly after the hardcover edition went out of print Dover Books issued a paperback reprint. The 1961 abridged edition has never gone out of print.

any other published assessment; but, like all the others, Cook rejected its main conclusions.

When Thompson published *On Growth and Form* in 1917 he had been Professor of Natural History at University College, Dundee, since 1884. University College was a struggling young institution that never did establish itself as a permanent entity: in 1917 it was merged with the University of St. Andrews. Thompson would spend the rest of his life at St. Andrews, where Pettigrew[2] had spent most of his career. According to Thompson's daughter (Thompson, 1958) he later referred to the Dundee period as "the years in the wilderness," because he had so acutely felt his isolation from the larger scientific and scholarly world. Thompson had applied without success for posts at more prestigious institutions. I think it is safe to say that the praise contemporary reviewers lavished on Thompson's book reflected their opinion of the book, not the prominence of its author.

By and large, reviewers' assessments of these two books reflected the mainstream viewpoint of British morphology in the early twentieth century, which I described in Chapter Two. Most scientists of the day accepted evolution as an established fact. Homology was seen as the central unifying concept of morphology, for

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[2]There is no evidence that Thompson ever met Pettigrew, but there are indirect connections between the two. Pettigrew gave public lectures in Dundee before University College was established, and was among the St. Andrews faculty who proposed its formation. After Pettigrew's death in 1908 his widow gave the University of St. Andrews £6000 to build the Bell Pettigrew Museum, where Thompson had an office from 1917 until his death in 1948.

it provided evidence of common ancestry. Most of the similarities between species reflected shared inheritance from a common ancestor. Differences resulted from adaptation to different environments. Some resemblances between species were probably not homologous; these resemblances, called "analogies," resulted from independent adaptations to the same functional need. In the early twentieth century many morphologists had doubts about Darwin's theory of natural selection, preferring one of several explicitly or implicitly teleological explanations for evolution. There was general agreement that most similarities and differences between species reflected either heredity or adaptation. Vitalism and creationism were no longer popular. The origin of life was a mystery (as it remains today), since no direct evidence was available. Whatever the origin of life, its evolution had been largely subject to physical laws. It was not yet known whether physical laws alone could explain life, but no living organism had ever been observed to *violate* physical laws.

As we saw in Chapters Three through Five, Pettigrew and Thompson diverged from this mainstream view in very different directions. For the most part, the differences between the reception of *Design in Nature* and the reception of *On Growth and Form* reflect these differences between their authors' viewpoints. Bonner (1961) remarked that Thompson's views on evolution "were heretic [*sic*] in 1917"; if Thompson was a heretic, then Pettigrew was a heathen.

I. Pettigrew's *Design in Nature*

Unlike most of his contemporaries, Pettigrew held that every species had been specially created by God, perfectly adapted to its particular environment. He considered the distinction between homology and analogy meaningless, because he saw it as based on a wholly arbitrary classification-scheme. Most biologists regarded homology *sensu* Owen as providing strong evidence in support of the notion that many of the similarities between species were due to shared inheritance from a common ancestor, or homology *sensu* Darwin. Pettigrew rejected any appeals to homology—*sensu* Owen or Darwin—because he could see no basis other than accepted taxonomic theories for distinguishing homology from analogy. If the taxonomic classifications were based on appeals to homology, and homology was defined on the basis of taxonomy, then was this not circular reasoning? Pettigrew thought the question answered itself. He did not divide similarities between species into any set of categories, because he considered all similarities to have the same epistemological status: proof of design. Every species had been created in a separate miracle by an all-powerful God who could and did suspend the operation of ordinary laws whenever He chose. Not only the origin of life but even its day-to-day operation required continuous divine intervention, for life could not be explained by ordinary physical laws.

A. The Reaction to Pettigrew's Views: Harsh Criticism

By and large, reviewers of Pettigrew's book were in general agreement: they repudiated Pettigrew's mode of practicing comparative anatomy. They saw it as an attack on the Darwinian concept of homology, which they considered the central concept of morphology. They were particularly critical of Pettigrew's assumption that any example of a particular shape proved the operation of the same cause. For instance, Pearl (1909) ridiculed the notion that all the diverse spirals described in Pettigrew's book shared a common cause. The writing—style and organization—of *Design in Nature* also got considerable criticism, but Pettigrew's positions on major issues seem to have been the primary reason reviewers disliked his book so intensely.

B. Reviews of Design In Nature

Four major periodicals published reviews of Pettigrew's *Design in Nature*. The least negative—one could hardly say favorable—of the four was an unsigned review in *Athenæum* (Athenæum, 1909). The anonymous reviewer saw Pettigrew's book as an updating of Paley's *Natural Theology*, arguing for largely the same conclusions by largely the same style of reasoning.

"However", the reviewer remarked, "since then the Darwinian theory, with all its corollaries, has appeared," and "for cogency of

argument we need only compare a section of the present work with a chapter from the *Origin of Species.*" Pettigrew, he alleged, stubbornly adhered to the "Mosaic [*ie.,* Biblical] account of creation," which was "not in agreement with the general trend of scientific thought of the day." Pettigrew's views, he opined, "afford an example of how individual judgment may be swayed by preconceived opinions in spite of evidence; for that there is a vast amount of evidence in favour of evolution and the influence of environment is undeniable." However, the book still "had some value for the student," for "Professor Pettigrew was an expert in human and comparative anatomy," and the anatomical data presented in his book were "accurate and up-to-date." Pettigrew's illustrations, he noted, deserved "unstinted praise" and the index was "excellent." Referring to the book's wealth of factual data, *Athenaeum's* review ends: ". . .though our convictions may remain unshaken by his arguments, we feel that Prof. Pettigrew has bequeathed to us a worthy record of his life's work."

Nature's unsigned review (Nature, 1909) was somewhat harsher than *Athenæum's* assessment. Like the others, the reviewer saw Pettigrew's approach to organic form as largely irrelevant to contemporary evolutionary biology. *Nature's* reviewer was also sharply critical of what he considered the book's excessive breadth of subject matter, for Pettigrew had "attempted a task which no one man could be expected adequately to perform." The result was as "broad

as the ocean, but lacking in depth" and poorly organized. For instance certain topics, such as "the telephone, bones of the hand and foot, spiral formations, and new theories of matter, are dropped rather at random in the middle of discussions with which they do not appear to have much connection." Because so many of its arguments were "distinctly unconvincing", the reviewer advised the reader to "only regard 'Design in Nature' as a memorial volume of the late Professor Pettigrew, and not to attach too great scientific value" to its reasoning and conclusions.

The last few paragraphs of the review sound a very different note from the rest. After a very negative account of the book, *Nature's* reviewer added that "since the above criticisms were written, a fresh aspect of Prof. Pettigrew's work has suggested itself to the present reviewer." In recent years, he noted, the popularity of anatomy as a field of study had declined markedly. Perhaps Pettigrew's "appreciation of beauty" might encourage more young people to study this "usually unpalatable subject."

Unlike the two reviews just described, an anonymous reviewer writing in the *Times Literary Supplement* (TLS, 1909) found Pettigrew's book devoid of merit. The reviewer began by stating his rather positivistic interpretation of scientific "laws," which he then contrasted with Pettigrew's view of natural laws. "The task of science is to describe, verify, and classify facts." A "law of nature" is "merely a description of an observed uniformity," as

opposed to a religious or social law, which is "a rule laid down for the guidance of an intelligent being by an intelligent being." The reviewer saw the theory of evolution as comprising laws of nature in the scientific sense: its statements fit the facts, and no other theory fit the facts nearly so well.

Pettigrew's book was "an exception to the general rule" because its author was "almost passionate in his rejection of modern science as conceived by modern men of science." For Pettigrew, "chance is any occurrence not immediately determined by the Deity, design is that which is manifested in *separate* acts of creation, law is lawyer's law, and order is that which results from the enforcement of edicts." This was not a scientific viewpoint; Pettigrew did not appear to have understood the theory of natural selection. Pettigrew interpreted 'natural selection' as meaning that organisms could select their own best characteristics for transmission to their offspring. *TLS*' reviewer was scornful: "never probably. . .was the theory of natural selection misinterpreted in a more extraordinary fashion." "Dr. Pettigrew," the review ended, "appeals to the same class of facts, indeed to the same facts, as Darwin and Wallace. But he denounces rather than meets the arguments of his opponents."

The review of *Design in Nature* by Raymond Pearl[3] (1909), which appeared in *Dial*, headed "On the Spirality of the Cosmos," is by far the most hostile and sarcastic review of a serious scientific work

that I have ever seen:

> The ponderous work on "Design in Nature," by Dr. J. Bell Pettigrew, is probably the most extensive and serious contribution to humorous literature which has appeared in recent years. It stands unique at this day and age. To find its peers, in respect of both matter and manner, one must go back to the period when the "Bridgewater[4] Treatises" flourished.

Pearl characterized the range of topics touched on by Pettigrew as "a most extraordinary collection of intellectual junk," since "one passes with absolutely no logical connecting links" from topic to topic. "In particular, Dr. Pettigrew was impressed by the universality of spirals in the cosmos," which he considered proof of design; to Pearl "this spiral philosophy" was "utter absurdity." The book represented an "enormous amount of labor," and it was "a pity that this labor should have been so largely wasted." "Seriously," Pearl concluded, "it is a matter for sincere thankfulness that the time is forever past when such a book as this could exert any significant influence on the thought or action of man," because "the day is long past when anyone can persuade men to a belief in a Higher Power by arguing that the Creator shows His infinite wisdom by fashioning men and corkscrews on the same plan."

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[3]Raymond Pearl (1879–1940), was a leading figure in early twentieth-century studies of growth and population biology. The bibliography of Lotka's (1924) classic text on mathematical biology has more citations to works by Pearl than by any other author. The chapter on rates of growth in Thompson's *On Growth and Form* also makes extensive reference to Pearl's work.

[4]The *Bridgewater Treatises* were a very popular series of books on natural theology published in the early nineteenth century. In 1829, the Earl of Bridgewater left £8000 to finance the publication of a work "on the power, wisdom, and goodness of God, as manifested in the Creation." The President of the Royal Society chose eight leading scientists, all prominent members of the British Association for the Advancement of Science, to write a series of treatises on this theme. They sold very well, and went through numerous editions.

The most sympathetic reader of Pettigrew's book was T. A. Cook[5] (1914), who made extensive use of *Design in Nature* as a source of examples for his own book on natural spirals, *The Curves of Life*. However, even Cook rejected Pettigrew's arguments. *The Curves of Life* is also of interest as an indirect link between *Design in Nature* and *On Growth and Form*. Thompson never cited Pettigrew's book[6], but he did cite Cook several times; therefore Cook's many references to *Design in Nature* provide strong evidence that Thompson must have known about Pettigrew's book.

Like Pettigrew's *Design in Nature*, *The Curves of Life* was an attempt to demonstrate that the ubiquity of spirals and related curves in nature and in art might reveal the existence of common underlying laws. However, Cook did not accept "that logical fallacy of design, which weakened the arguments drawn by the late Professor Pettigrew from so much of his most brilliant original research." (Cook, 1914:437). "I do not ask you to believe that the occurrence of similar curvilinear formations and spirals in various organic and inorganic phenomena is a proof of conscious design," Cook wrote. "I only suggest that it indicates a continuity of process imposed by the operation of universal laws" (Cook, 1914:4). Unlike Pettigrew,

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[5]Sir T. A. Cook (1867–1928) was not a scientist, but a journalist and art critic. Thompson cited his 1914 *Curves of Life* as an excellent source for examples of spirals, and reproduced one of his illustrations. Cook made no secret of his lack of specialized training; he expected that "every specialist will delightedly correct those errors which occur in ground familiar to him" (p. 2).

[6]The one reference to Pettigrew in Thompson's *On Growth and Form* is to Pettigrew's early work on the arrangement of muscle fibers in the heart and other organs.

Cook conceded that "it may be only an accident" (p. 408) that such similar spirals appear in such diverse contexts. Though he himself suspected that such resemblances were not accidental, he thought only scientific investigation (which he was not able to undertake) could determine the actual causes of the geometrical regularities his book described. Certainly Cook believed that the process of natural selection must somehow be involved in the formation of organic spirals structures.

II. Thompson's *On Growth & Form*

Although Thompson (like Pettigrew) was critical of mainstream evolutionary theories, and reviewers did not entirely agree with his views, they found *On Growth and Form* both valuable and interesting. Pettigrew seemed to be rejecting standard evolutionary theories out of hand; as we have seen, contemporary reviewers disliked *Design in Nature* for just this reason. Thompson, by contrast, was perceived as engaging in an informed and useful dialogue with contemporary morphologists.

Thompson was an evolutionist, and he conceded that references to homology (*sensu* Darwin) and adaptation were sometimes defensible, and that the concepts were embedded in useful morphological theories. However, as we saw in chapter five, he thought many aspects of biological form could be understood independently of the notions of heredity or adaptation as direct effects of physical

forces on organisms. Thompson's method for studying a form began by seeking a detailed mathematical description of it. Once a simple geometrical description of its geometry had been found, he would then search for non-biological systems that produced the same shape. If a simple mechanism could produce a given shape, there was then no justification for assuming that anything beyond the operation of ordinary physical laws was required to explain the morphology. In practice, however, very few biological forms could be simulated exactly by such models, so most aspects of biology remained too complex and too poorly understood for mechanical models to be devised. Nevertheless, since no aspect of life was known to violate physical laws, Thompson held that the proper scientific procedure was to seek mechanical models before proposing any other mode of explanation. Life might ultimately turn out to be outside the scope of the laws of inanimate matter, but science could only learn whether it was by starting from the assumption that it did not. Thompson was very critical of contemporary evolutionary theories—whether Darwinian selectionism or some more explicitly teleological model—because they did not provide mathematical descriptions or mechanical models of how organic forms grew, developed, and evolved. In this respect Thompson saw contemporary evolutionism as being too much like nineteenth-century natural theology.

A. The Reaction to Thompson's Views: Praise, With Reservations

Contemporary reviewers were impressed by the ingenuity of Thompson's models, the scope of examples with which Thompson illustrated his method, and the elegant prose in which his ideas were expressed. Thompson's mathematical approach to form, reviewers agreed, shed valuable light on many aspects of morphology. Thompson's book also convinced them that some aspects of morphology probably could be described in mathematical equations and explained by physical arguments. But while reviewers appreciated the need to seek mechanical explanations of biological forms before resorting to specifically biological modes of explanation, they felt that Thompson had overstated his case. Yes, they agreed, the search for mechanical models was both valuable and interesting—and Thompson's book was one of the strongest arguments for that approach ever published. However, they saw Thompson's approach as a supplement to existing theories of evolution, not as an alternative to them. This general view—that Thompson had overstated the case for direct physical causes in morphology—has been echoed and amplified by more recent critics. Modern experimental research has convinced recent critics that living organisms are far more complex than Thompson realized, and therefore that his models are much too simple to explain how organisms develop and evolve.

B. Reviews of On Growth & Form

Unlike Pettigrew's *Design in Nature*, which was posthumously published and never reprinted, Thompson's *On Growth and Form* went through two editions in the author's own lifetime (as noted above), and since the second edition, appearing in 1942, has remained almost continuously in print. Not only was the book reviewed by contemporaries, but in recent decades several leading scientists have published essays praising it and assessing its continuing influence on morphology. While my primary focus must naturally be on contemporary reactions to the first edition, later evaluations of the book also deserve brief comment.

1. Reviews of Thompson's first edition (1917)

Four major periodicals carried reviews of Thompson's first edition, all printed in 1917 and all highly favorable. While three reviews of *Design in Nature* were unsigned, only one review of *On Growth and Form* was unsigned—in the *Times Literary Supplement* (TLS, 1917). "Professor D'Arcy Thompson," this review began, "has written an interesting and valuable book on a topic of enduring interest." The reviewer was obviously impressed by Thompson's book, but he had one main reservation: he was critical of Thompson's "apparent belief that he is proposing a new organon which shall displace all existing theories." Instead he saw Thompson's approach as a potentially valuable supplement to traditional morphology: "by all means let

physical solutions be exhausted first, but such a method of inquiry continues rather than opposes the patient spirit of Darwin."

Thompson's subject (how to explain unity and diversity in the forms of organisms) was, in the reviewer's eyes, old but still important. "Any schoolboy" could explain homologous resemblances by reference to shared inheritance from common ancestors. "Professor Thompson, even in his most critical mood, would give some marks for such an answer; but, as a learned anatomist, he would know that it did not carry us very far." Some resemblances, known as analogies, did not appear to result from shared inheritance, and "the systematist who is trying to put creatures in their proper places on the family tree is always getting into trouble." While neither "popular judgment" nor scientific opinion had yet agreed which of several explanations of strictly analogous resemblances was correct, most of the theories then under consideration shared an element of teleology:

> Things are alike or different because it is good that they should be alike or different, that is to say, good for the things themselves. . .Professor Thompson asks us to consider if it not be the case that in a very large number of instances animals and plants or their parts are alike or different not because it is useful that they should be alike or different but because they must be so. . .resemblances are the result of similar forces acting on similar materials; differences happen when dissimilar forces impinge on the same material, or. . .when similar forces impinge on dissimilar material.

TLS' reviewer characterized Thompson's book as an attempt to explain the "must be so" above by reference to mathematics and physics, using numerous examples to show that many organic forms had their analogues among inorganic ones. Thompson's main point, as

summarized by *TLS*' reviewer, was that:

> The zoologist must begin with mathematics; it is only when he has satisfied himself that a form or magnitude, an arrest or a proliferation, is not the immediate consequence of simple and known factors that he is entitled to suggest purpose or design, blood-relationship or its absence.

This point, the reviewer agreed, was well-taken. He might disagree with Thompson concerning the extent to which physical causes (rather than heredity or adaptation) had molded the forms of organisms, but Thompson's book did demonstrate how physical modelling could sometimes be a very useful adjunct to standard morphological approaches.

While *TLS*' review focused on general principles, J. Arthur Thomson's[7] 1917 review (published in *Nature*) focused on Thompson's specific examples. Whereas *TLS*' reviewer expressed general skepticism about the ability of abiotic factors to explain morphological laws, J. A. Thomson cited specific exceptions—aspects of morphology that did not appear to fit Thompson's theory. Like the other reviews, J. A. Thomson's review began with very high praise for *On Growth and Form*:

> This book, at once substantial and stately, is. . .an achievement for its distinguished author to be proud of. It is like one of Darwin's books, well-considered, patiently wrought-out, learned, and cautious—a disclosure of the scientific spirit. It is an application of some of the concepts of physical science and sundry mathematical methods to the study of organic form.

J. A. Thomson was impressed by Thompson's elegant

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[7] *Thomson* without a p, not *Thompson* with a p. To reduce confusion, in my summary of this review I will refer to *Nature*'s reviewer as J. A. Thomson while referring to D'Arcy Wentworth Thompson as simply Thompson.

illustrations of mathematical analysis (such as the "attractive chapter" on logarithmic spirals) and physical modeling, but he added that "the author has dwelt most on those aspects of organic growth which have their analogies among inanimate things." In his summaries of Thompson's mathematical models, J. A. Thomson pointed to issues of organismal biology that he felt such modeling did not address—particularly the often exquisitely subtle (and not very well understood) mechanisms of physiological regulation and of heredity. Because Thompson said little about such specifically biological topics, J. A. Thomson wrote, "we were tempted to say 'magnificent but not biology' but wiser reflections prevailed," stating that Thompson may have focused too much on one aspect of biology, but that his book was indeed about biology, and that what it did, it did very well, and that Thompson was due "felicitations on his masterly book," which provided a "fresh revelation of the unity of nature"

H. W. Carr, in his review for the *Hibbert Journal* (Carr, 1917), described the book as "a treatise on the mathematics of biology." In general, his review of *On Growth and Form* was very similar to J. A. Thomson's. Like the others, it began with high praise:

> It is clear and lucid, and deals with problems of enormous, often of surprising, interest—problems of science and problems of philosophy. The exposition is so admirable that no one need fear that the mathematics will obscure for him the philosophy, or the philosophy the science, or the science and philosophy the mathematics. To every thoughtful person growth and form are a subject of constant wonder.

Like J. A. Thomson's review, Carr's was organized around specific

examples of Thompson's method rather than around general principles. As did J. A. Thomson, Carr noted that Thompson's method did not bear upon some important aspects of biology, but he was somewhat less critical of the book on this point:

> Whether or not the student is satisfied with this attempt to explain the phenomena of biological change by showing that they can one and all be brought within the range of known physical actions, or at least that known physical phenomena produce similar effects, there can be no doubt as to the soundness of the scientific procedure. If, as many hold, [mechanical modeling] leaves, and of necessity must leave, the vital principle itself untouched, nevertheless it is work of supreme importance in itself and productive of knowledge, and it is not easy to see how it could be obtained by any other method. If anyone is in doubt he has only to read this book.

Near the end of his review, Carr noted again that "the striking success and the amazing simplicity and beauty of the results will silence at once any skeptical doubt as to the utility of the method." However, "throughout the whole inquiry," Carr did feel an "intense longing to know what life itself is. That need is not satisfied by the scientific study of growth and form, useful and profoundly interesting as it is."

Unlike the other reviews of *On Growth And Form*, the review published in *Science* (McMurrich[8], 1917) did not temper its praise with reservations. McMurrich saw the book's purpose as showing "that throughout the whole range of organic morphology there are innumerable phenomena of form which are not peculiar to living things," "This thesis," McMurrich remarked, "Professor Thompson elaborates in a most interesting manner, developing with the aid of

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[8]The review was signed "J. P. McM." This was almost certainly the prominent Canadian anatomist and historian of anatomy James Playfair McMurrich (1859–1939).

our fuller knowledge of physical forces. . .the mode of study initiated by Borelli." He noted Thompson's scholarly thoroughness in acknowledging predecessors, whose results "receive clear exposition, but the work is far from being a mere compilation, a refreshing originality being characteristic both in subject matter and in the manner of its presentation." He characterized the book as "one of the strongest documents in support of the mechanistic philosophy that has yet been put forth." Because his review was quite brief—only a page and a half—he admitted that it would be impossible to provide an adequate summary of the book, "filled as it is with facts and ideas of the greatest interest to morphologists." He confined himself to giving a few of Thompson's examples[9] a "mere mention." Of course, "this brief outline" could not do justice to the richness of content or the "clearness of expression which makes every page of interest." McMurrich ended his review by recommending the book as "revealing food for thought and fields for investigation which have been too much neglected by students of morphology."

2. Reviews of Thompson's second edition (1942)

The second edition of *On Growth and Form* did not attract as much attention from the scientific community as had the first edition. Several periodicals[10] carried very brief notices, but I have found only two extended reviews of Thompson's second edition that were

[9]As with many commentators, Thompson's treatment of the logarithmic spiral was briefly noted in this review.

published in his own lifetime: one by Dorothy Wrinch (1943) in the history of science journal *Isis*, and one by the noted philospher of science and logician Ernst Nagel (1945) in the *Journal of Philosophy*. This suggests that working scientists at this time did not see the book as immediately relevant.

Wrinch, for her part, thought morphologists should have seen the importance of Thompson's book long ago; her review of Thompson's second edition was mostly devoted not to analyzing the content of his book but to criticizing twentieth-century morphologists for having failed to incorporate Thompson's insights into their science. "It is remarkable that *On Growth and Form* should have appeared as early as 1917," she commented. Morphologists were still not accustomed to thinking quantitatively, so "they were poorly prepared to face the constructive iconoclasm of Sir D'Arcy's book." Particularly radical, in her view, was

> the therapy presented for dislocated phylogenetic concepts. With this ailment endemic, biology as a whole was not prepared for an analysis of form into components of two types: those for which biological history is relevant and those that remain, wherever found, specific antecedent properties of the spaces within which and the materials from which, organisms necessarily fashion themselves. Without benefit of true physical insight, it was difficult also to grasp the significance of mere size.

Even in recent textbooks, Wrinch complained, "cilia and flagella are still being operated like small horse-whips." No author who had read and understood *On Growth and Form* could possibly

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[10]Periodicals printing brief reviews of Thompson's second edition included *American Anthropologist 45*:293 (April 1943), *The New Yorker 18*:72 (12 September 1942), and *Queens Quarterly 49*:410 (1942).

make such errors. But it was the way morphologists focused on phylogeny that Wrinch saw as the main barrier to progress: "had they understood the real purpose of *Growth and Form*, comparative anatomy would not have become a dismal discipline—useful to be sure, but nurtured as well as hampered by a repertoire of exactly one idea." While Thompson was always far more diplomatic in his choice of words, Wrinch here echoed Thompson's main criticism of orthodox evolutionary morphology: its tendency to regard the historical *description* of evolution as providing a sufficient causal *explanation*. Thompson, said Wrinch, "refuses to be either more or less impressed by differences than by resemblances." Both, she thought, "require explanation" in terms of physical forces and the materials on which those forces act.

Ernst Nagel (1945) characterized *On Growth and Form* as a "remarkable and subtly influential work." Since "it is not a treatise in philosophy" but a book about morphology, "only a specialist in biology can evaluate" its scientific content in any detail. "Nevertheless," Nagel went on, "it deserves a notice, if only a short one, in a philosophical journal, for it is unusually significant for any generalized conception of the world we inhabit." He summarized Thompson's main theme as follows:

> the form of an object is conceived by Thompson as a "diagram of forces," from which the forces that are acting or have acted upon an object may be inferred. This conception is illuminatingly illustrated with amazing but gracefully carried learning through an analysis of an almost endless variety of phenomena taken from practically every field of biological inquiry (genetics being one of the notable exceptions). Thompson believes that teleological explanations constitute *one* way in which we may sometimes understand how things came to be. But in the present book, at any rate, he

> looks upon organic forms as a physicist would; that is, he looks upon them as *mechanisms* which control and guide into determinate paths the workings of energy...without engaging in explicit polemics with protagonists of vitalism he nevertheless shows the irrelevance of this doctrine to biological research.

Like the others, Nagel's review ended on a note of praise. Thompson's book was "a modern confirmation, written in magnificent prose, of Galileo's aphorism that 'the Book of Nature is written in characters of geometry.'"

3. Later Assessments of Thompson's Work

From 1917 to 1945, reviews of *On Growth and Form* published during Thompson's lifetime generally combined high praise for Thompson's mathematical analyses of form, and even higher praise for his writing, with skepticism about the power of his physical models to explain the wide range of morphological phenomena that Thompson had tried to explain. Later commentators share this general viewpoint, but two novel themes are present in many later appreciations. First, of course, more recent writers have had the advantage of knowing—as Thompson's contemporaries could not—the directions morphological research was to take in later decades. Second, many later writers favor a reinterpretation that retroactively endows Thompson's models with great explanatory power by integrating them into a paradigm that Thompson had never accepted—the modern evolutionary synthesis of the 1930s and 1940s.

The first to propose such a reinterpretation was G.E.

Hutchinson (1948). Like earlier critics, he thought Thompson's mechanical models, elegant as they were, did not have sufficient explanatory power. Many of them seemed "simple, direct, and yet entirely unconvincing." Thompson had "accepted adaptation only where it would be impossible to deny it. . .and then was at a loss to explain how it had come into being." Given Thompson's reluctance to accept historical modes of explanation, "he had either to provide a mechanical explanation, or admit that the phenomenon before him was outside his realm." Many of the forms that Thompson had tried to explain in mechanical terms—as direct responses to the stresses induced by external loads—were most likely hereditary, for their embryonic development took place even in the absence of any applied loads. "Forbidden a Lamarckian interpretation," Hutchinson noted, it seemed "difficult to account for the phenomenon in mechanical terms."

Hutchinson found an ingenious resolution of this difficulty. He agreed with Thompson that mechanical forces had indeed played an important role in the evolution of many organic forms, but he also agreed with Thompson's contemporaries—and later morphologists—that the development of an individual organism was largely controlled by internal, inherited factors (*i.e.*, genes). The role of mechanical forces in evolution had been mainly as an important part of the selective environment, not as a direct cause of evolution. "Equilibrium forms," such as Thompson had described, were "common in

organic nature because any organism not exhibiting them would have to be elaborately protected in other ways against deformation by the stresses and strains imposed by the environment." This reinterpretation Hutchinson "offered more in order to remove[11] impediments to the study of the book, than as criticism of a great man who has died." And Hutchinson meant that "great"; he considered *On Growth and Form* "one of the very few books on a scientific matter written in this century which will, one may be confident, last as long as our too fragile culture."

P. B. Medawar (1958) expanded upon this neo-Thompsonian[12] view of form, in which the influence of physical forces upon biological processes was mediated by selection and heredity:

> we need not doubt that D'Arcy's forces acted once upon a time in determining the pathway of evolution, but if that is so, then the problem is just what D'Arcy supposed it not to be: a matter of history. The whole point is that the forces which did at one time shape limbs, or set the limits within which the shapes of limbs must fall, were translated into those developmental *instructions* about limb-making that now form part of our genetic heritage. . .no one denies the essential truth of what D'Arcy Thompson had to say about the importance of physical and mechanical forces; he simply mistook their context.

Medawar also added his own notes of ringing praise for Thompson's writing to the ever-growing chorus: "*Growth and Form* is beyond comparison the finest work of literature in all the annals of science that have been recorded in the English language." This he

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[11]Original reads ". . .to removed [*sic*] impediments. . . ," which seems an obvious typographical error.

[12]"Neo-Thompsonian" is my phrase, not Medawar's. I do not know whether Medawar arrived at this view independently of Hutchinson; in any case the important point is that this reinterpretation of Thompson's theory appeared only after his death. Reviews of *On Growth and Form* published during Thompson's life noted the difficulty but not its resolution.

saw as Thompson's most important contribution to scientific literature; for this alone his book would be forever worth reading.

Bonner's (1961) appreciation of Thompson's book quoted extensively from both Hutchinson and Medawar. After quoting Medawar on the excellence of Thompson's prose, Bonner added, "I do not think this very high praise unjustified." Like Medawar, he saw Thompson's influence on science as largely indirect. Like both Hutchinson and Medawar, he favored a selectionist interpretation of the correspondences between physical forces and biological forms that Thompson had so ably identified, in order "to show how the heterodoxies of D'Arcy Thompson can be easily transformed into orthodoxy." Bonner's appreciation of Thompson differed from earlier ones mainly in being much more detailed. It was his introduction to his own abridged edition of *On Growth and Form*. As one who had examined every word of the original to decide which ones should be cut, he had naturally studied the book with considerable care.

Stephen Jay Gould's (1971) essay made frequent reference to Hutchinson, Medawar, and Bonner (describing their essays as "the best three of the many articles written to celebrate *Growth and Form*"). In general Gould echoed their assessments, adding details drawn from his own research in evolutionary biology. Without denying Thompson's limitations, Gould's essay (like Wrinch's before him) emphasized the extent to which evolutionary biology had *still* failed to incorporate Thompson's key insights. Many evolutionary

theories emphasized such non-morphological concepts as gene frequencies and reproductive success while seemingly forgetting that genes must affect bodies in some manner if they were to have any impact on reproductive success or survival. On the other hand, those among Gould's contemporaries who studied actual forms often ignored their functional and mechanical aspects. "Pure description," Gould complained, was "as firmly rooted in theory as the most abstract and mathematical approach to form," but the theory was hidden and ignored Thompson's insights. "I believe," Gould wrote, "that a science of form is now emerging and that D'Arcy Thompson will be regarded as its godfather."

III. Present Reception

As we have seen, Pettigrew's *Design in Nature* was universally rejected in its own day, and soon forgotten. Its lack of scientific impact seems predictable given the extent to which Pettigrew rejected the key biological and methodological assumptions of contemporary biology. It has been very different with Thompson's *On Growth and Form*. While Thompson's viewpoint was not the same as that of his contemporaries—and biologists in later decades have continued to differ with Thompson on several crucial points—scientists throughout the twentieth century have praised his book. Even when they disagree with Thompson, most commentators find challenging insights that enliven their own thought. Today, Thompson's theory of form remains outside the mainstream, but his

criticisms of Darwinian evolutionism still seem relevant and important.

Last year (1992) Cambridge University Press issued a new reprint of J. T. Bonner's abridged edition of *On Growth and Form*. Gould was invited to write a preface, and Bonner wrote a brief addendum to his introductory essay. Both have used the opportunity to reevaluate their earlier essays. Gould remarks that in his 1971 essay, "I misread him (or grasped him only partially) as a consequence of my misguided romanticism." Thompson had been right to criticize his contemporaries, for reasons that remain important even today. However, Gould notes, "Thompson was also a man of his own age, and I missed this theme." Many in Thompson's day had shared his doubts about natural selection, doubts that mainstream biologists now regard as resolved[13].

Bonner notes that "quite extraordinary progress" has occurred in many areas of biology since he wrote his 1961 introduction; these changes have affected not only molecular biology, but also areas closer to Thompson's own heart. The "new accomplishments of biology do not supplant D'Arcy Thompson's message: they complement it." In particular, Bonner notes that attention is now shifting from

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[13]This consensus, though quite strong, is by no means unanimous. Messon (1991) provides an excellent summary of present-day non-Darwinian *scientific* theories of evolution, which should not be confused with the "creation science" of Biblical fundamentalism. I do not entirely agree with Messon's views, but his book does represent a serious, knowledgeable critique of modern evolutionary biology. It bears little resemblance to the anti-evolutionary tracts of Gish (1972) and his ilk.

describing the genes themselves to analyzing how genes direct growth and development. Thompson may have missed the importance of genes to evolution; molecular biologists are now rediscovering the importance of mechanical forces. "Neither the role of natural selection nor the laws of physics can be ignored; together they are responsible for development and evolution," Bonner remarks. For this reason, Bonner contends, Thompson's message "glows even more brilliantly in the 1990s than it did in the 1960s" (or earlier decades, I would add).

CHAPTER 7

Summary

The twentieth century has seen tremendous changes in all areas of science in general and biology in particular. Social and institutional structures have also changed radically, so biologists of the late twentieth century inhabit a world that is very different from the turn-of-the-century world inhabited by Pettigrew and Thompson. The basic assumptions, methods for doing research, and central questions of morphological thought have changed with the times. Despite all these changes, to a considerable extent the perspective of history validates the reception accorded Pettigrew's *Design in Nature* and Thompson's *On Growth and Form* by the authors' contemporaries.

The Early Twentieth Century

When the twentieth century began, Darwin's theory of natural selection was still not widely accepted by biologists. Nevertheless, few doubted that species now living had *evolved*, by descent with modification, from ancestral species. Morphological research was dominated by the search for genealogical relationships among species. Therefore, since Pettigrew's book was so obviously intended as an attack on all forms of evolutionary theory, most reviewers were extremely unsympathetic. They felt little sense of engagement between Pettigrew's arguments and contemporary concerns

of their science. Even T. A. Cook, who was considerably more sympathetic to Pettigrew's views on spirality than anyone else, regarded Pettigrew's main arguments as fallacious.

Thompson's book, by contrast, was seen as an informed and valuable critique of contemporary morphological science. Despite certain reservations about Thompson's somewhat unconventional evolutionary theory, contemporary reviewers found his ideas stimulating and important. Thompson was careful to emphasize that he was not attacking evolution in general, but merely pointing out aspects of biological form that he felt had been somewhat neglected in the general focus on heredity and adaptation. Even those who emphasized the limitations inherent in Thompson's theory of form felt a strong sense of engagement with the current concerns of their science. Thompson's theories might not explain all the phenomena that Thompson attempted to explain, but Thompson's book did convince reviewers that physico-mathematical analysis could make important contributions to the science of comparative morphology.

Later Decades

As we have seen in earlier chapters, by 1914 Pettigrew's *Design in Nature* had been largely forgotten[1] by the scientific community. None of the many changes in science since 1917 have been in directions resembling those advocated by Pettigrew; present-day textbook orthodoxy is even farther from the views advocated by *Design*

in Nature than was the scientific consensus of 1908. I have been unable to find any work published after 1914 that makes significant use of Pettigrew's book.

Thompson's book, on the other hand, remains in print and continues to receive nearly the same combination of praise and criticisms as it did in 1917. In recent decades, evolutionary thought has been dominated by the "modern synthesis" of natural selection and population genetics. Since—most evolutionary biologists now believe—the modern synthesis has resolved the main difficulties most of Thompson's contemporaries had with Darwinian selectionism, modern commentators have placed great stress on reinterpreting Thompson's theory of form in a manner consistent with modern selectionism. Thompson believed the mechanical forces imposed on organisms by their environments often played a direct role in molding their forms. Modern commentators, like Thompson's contemporaries, believe that heredity plays a much greater role in morphology than Thompson believed. Instead of directly molding organisms, most modern commentators believe, the external forces identified by Thompson have formed an important part of the

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[1]The modern neglect of *Design in Nature* has certainly not been because copies of the book are difficult to find in libraries. In a diligent but far from exhaustive search of US academic library catalogs, I located research libraries in 36 states and the District of Columbia with copies. I used three methods to search US libraries: (1) the printed *National Union Catalog* issued by the Library of Congress, (2) the OCLC interlibrary network, and (3) remote searches of many individual library catalogs via the Internet. The first edition of Thompson's book is much harder to find; only 500 copies were printed and most of those are in private collections. The Interlibrary Loan office at Duke's Perkins Library had considerable difficulty obtaining a copy of Thompson's 1917 edition for my use. Later editions of *Growth and Form* can be found in most large bookstores.

selective environment under which the ancestors of present-day organisms evolved by natural selection. Improved knowledge of such fields as genetics, development, evolution, and physiology has led modern commentators to be even less willing than Thompson's contemporaries to accept his direct causation theory.

Future Prospects

The mainstream viewpoint of today is, if anything, even farther from Pettigrew's views than was the mainstream view of 1908, and I see no prospect of *Design in Nature* ever being seen as an important scientific work. On the other hand, I agree with Gould and Bonner that the prospects for *On Growth and Form* seem as bright today as ever. The issues addressed by Thompson's book are, if anything, attracting more scientific interest today than in Thompson's own lifetime. At present I cannot say whether Messon (1991) is right that the synthetic theory will soon be replaced by something else, though I personally doubt that will happen. The limitations of efforts to understand evolution in such non-morphological terms as those of genetics and population biology do seem increasingly evident. I agree with Bonner that Thompsonian physico-mathematical analysis, when integrated with what is now known about heredity, promises to make major contributions to the modern study of growth and form. Perhaps in the 1990s we shall finally fulfill the prediction of Gould (1971) "that a science of form is now emerging, and that D'Arcy Thompson will be seen as its godfather."

Because biology in recent decades has been so visibly dominated by astonishing progress in areas other than morphology, many scientists have seen the study of morphology as rather old-fashioned, and some historians have accepted this view. As we saw in Chapter Two, Garland Allen (1975) characterized twentieth-century biology as a "revolt from morphology." Bynum (1981:152) remarked that "form is now the preserve of taxonomists and evolutionary biologists." If— as I personally expect—biology in future years sees a revival of scientific interest in the issues that Thompson saw as central to morphology, then this view of morphological research as obsolete will also change. If the present revival of scientific interest in Thompson's *On Growth and Form* continues, I expect there will also be an increased interest among historians of science in Thompson's life and work.

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Biography

Matthew David Healy was born in LaCrosse, Wisconsin, on September 14, 1960. He was graduated from Marquette University High School in Milwaukee, Wisconsin, in May 1978. He attended Purdue University, West Lafayette, Indiana, from 1978 to 1982, receiving his B.S. in Engineering in May, 1982.

He was employed as a Product Engineer by Siemens Energy and Automation, Inc., Atlanta, Georgia, from 1982 to 1985. He attended the University of Wisconsin-Milwaukee in Spring Semester 1985. He attended the Summer in Rome, Italy, program of Louisiana Tech University in 1985.

From 1985 to 1994 he has been enrolled in the Ph.D. program in Zoology at Duke University, Durham, North Carolina. From 1985 to 1990 he was a Zoology Teaching Assistant at Duke.

He married Kimberly Coleman on August 3rd, 1991. Since July, 1992, he has been employed as a research associate in the laboratory of Professor David Ward, Department of Genetics, Yale School of Medicine.